SWG Final Report: Factors that influence invasion of nonnative brook trout (*Salvelinus fontinalis*) and their displacement of native cutthroat trout (*Oncorhynchus clarkii*) in the Northern Rocky Mountains

Bradley B. Shepard

Montana Department of Fish, Wildlife & Parks
1420 East Sixth Avenue
Helena, Montana 59620-0701

Montana Cooperative Fishery Research Unit
Ecology Department, Montana State University
Bozeman, Montana 59717-3460

Final Report

2009

Executive Summary

Inland native cutthroat trout subspecies have declined throughout their ranges, including the two subspecies (westslope, *Oncorhynchus clarkii lewisi*, and Yellowstone, *O. c. bouvieri*) that occur in Montana. Two major reasons for these declines include loss or degradation of suitable habitats and interactions with nonnative trout species, particularly brook trout. Our goal for this study was to identify habitat conditions that promote persistence of westslope and Yellowstone cutthroat trout in the Northern Rocky Mountains. Specific objectives were to: (1) determine if nonnative brook trout and native cutthroat trout occupy similar habitat niches in Northern Rocky Mountain headwater tributaries; (2) illustrate whether stream habitat restoration strategies commonly used in Montana are effective in increasing abundance of cutthroat trout; (3) evaluate how habitat condition interacts with brook trout presence and abundance to affect the abundance and distribution of cutthroat trout; and (4) assess the effect of presence of non-native fishes on success of cutthroat trout habitat restoration projects. We also investigated whether nonnative brook trout and native cutthroat trout consumed the same prey items during the summer.

We investigated whether 75 mm and longer westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) occupied a niche similar niche to 75 mm and longer brook trout (Salvelinus fontinalis) by comparing biomasses, population densities, and individual fish condition factors prior to and following total removal of brook trout in reaches (2.3 to 3.0 km) of three headwater streams in Montana. We present a new method for estimating standing crops and their associated errors using depletion estimators. Total trout biomass did not change significantly after brook trout removal indicating that these two species have similar niches in these streams. Densities of juvenile westslope cutthroat trout were significantly and negatively affected by densities of juvenile brook trout and positively related to densities of adult westslope cutthroat trout, based on linear model testing (R^2=0.482; F-ratio=15.415; P<0.001). Including densities of westslope cutthroat trout or brook trout from the previous year did not measurably improved model performance. We found that densities of juvenile brook trout negatively affected body condition of juvenile westslope cutthroat trout using two separate analyses. We found evidence for size-asymmetric competition in one stream, but not in the other stream where size-asymmetry was tested. Our results indicated that interspecific competition between brook trout and westslope cutthroat trout was nearly as strong as intraspecific competition within westslope cutthroat trout, especially among juveniles, providing insight into one mechanism by which brook trout displace westslope cutthroat trout.

We found 440 habitat restoration projects in the Montana FWP database that had been started and completed between 1995 and 2006. Of these projects 55 involved some type of stream channel restoration that included construction of pool habitats and 35 projects had instream cover additions associated with them. Our analyses of fish abundance estimates in habitat restoration treatment and nearby control sections indicated that while habitat restoration often increased densities of both cutthroat and brook trout, the proportion of brook trout was often higher within habitat restoration sections than in control sections, especially when instream cover (usually woody debris)

was added as part of the restoration project. These findings were more obvious in streams where brook trout had become well established. We also found that habitat restoration projects generally increased average individual body condition of both brook and cutthroat trout, but that these results varied across different projects and streams.

Food habits data suggested that westslope cutthroat trout in allopatry consumed relatively higher proportions of Ephemeropterans than cutthroat trout in sympatry with brook trout. Cutthroat in sympatry with brook trout fed more heavily on terrestrial adult insects off the water's surface. We speculate that brook trout might be displacing cutthroat trout from deeper water benthic positions and forcing them higher in the water column where they fed on surface insects and might also be more vulnerable to predation.

Table of Contents

Introduction

Invasion by exotic species has led to dramatic changes in native biological communities and has been implicated as a major cause of extinctions (e.g. Miller et al. 1989; D'Antonio and Vitousek 1992), especially within freshwater ecosystems (Arthington 1991; Reinthal and Stiassny 1991; Townsend 1996; Claudi and Leach 1999; Fuller et al. 1999; Kolar and Lodge 2001; Spens et al. 2007). Invasive species affect native species primarily through competitive and predatory interactions among species (Elton 1958). While negative impacts of non-native species on native species are well documented, ecological outcomes of invasions can vary widely (Elton 1958; Burger et al. 2001; Dunham et al. 2002a). Invasion of exotic fish species have been due to intentional releases of exotic sport fish by fish managers to increase recreational opportunities, unintentional releases by anglers or fish managers, illegal or unauthorized releases by the public, and natural dispersal of exotic fish after their release (Cambray 2003). Aquatic invasions tend to homogenize freshwater communities (Rahel 2000 and 2002; Marchetti et al. 2006; Taylor 2004).

Theoretical models suggest the invasion of nonnative freshwater species is facilitated through the interaction of three factors: biotic resistance, habitat quality, and connectivity (Moyle and Light 1996; Benjamin et al. 2007). An important goal of invasion biology is to identify physical and environmental characteristics that may make a region particularly receptive or resistant to invasions (Marchetti et al. 2004).

Invasion success for particular species may be predictable (Case 1996; Grosholz and G. M. Ruiz 1996; Townsend 1996; Gido et al. 2004); however, some authors suggest this is often not the case (Mack et al. 2000). If prediction is possible, managers could use this predictability to better conserve native species and habitats critical to their persistence (Gido et al. 2004). Landscape clines, such as altitude (Pysek et al. 2002; Pino et al. 2005), climate (Pino et al. 2005), and the existing biotic community likely regulate invasion success for individual exotic species (Meekins and McCarthy 2001; Gido et al. 2004; Pauchard and Alaback 2004). Identifying habitats critical for native species, especially those habitats that are also resistant to invasion by exotic species, may provide important conservation opportunities.

Byers and Noonburg (2003) suggested that accounting for scale might be important when conducting invasion studies, as they found that native and exotic species diversity were often positively correlated in large-scale observational studies but negatively correlated in small-scale experimental studies. Thus, it will probably be necessary to identify habitats critical to native species at various spatial scales, from broad, range-wide scales down to microhabitat scales, so managers can apply the appropriate conservation measures at the appropriate scale (Laurance 1997; Pino et al. 2005).

Documented impacts of exotic fish on native aquatic communities include reduction or extinction of native aquatic species, alteration of habitat, and introduction of parasites or disease organisms (Krueger and May 1991; Ross 1991; Vander Zanden et al. 1999;

Taniguchi et al. 2002; Leyse et al. 2004; Vander Zanden et al. 2004). However, some studies have shown no significant impacts of exotic fish on native communities (Wissinger et al. 2006). Competitive interactions between invasive and native species have generally been considered among the most important mechanisms driving invasion dynamics, but such interactions are often poorly understood (Byers 2000; Dunham et al. 2004; Thompson 2004).

Studying ecological interactions during and following establishment of exotic species will provide insights into: 1) how invasion affects communities (Bohn and Amundsen 2001) and, 2) what managers might do to eliminate or reduce the risk of exotic invasion, especially if we identify life history stages where management will be most effective (Sakai et al. 2001; Taniguchi et al. 2002). Invasive species also offer excellent opportunities to study basic processes in population biology (Sakai et al. 2001). Lambrinos (2004) reviewed studies on the interaction between ecology and rapid evolution that might occur during invasion, for both the invading exotic species and the extant native species, and concluded that at least in some situations an explicit understanding of the contemporary co-influence of ecology and evolution might produce more effective and predictive control strategies.

Peterson and Fausch (2003) demonstrated how a conceptual framework could be used to design a manipulative field experiment to test for population-level mechanisms causing ecological effects and promoting invasion success. They suggested that experiments of this type could provide invasion ecologists a useful example of how a taxon-specific invasion framework can improve the ability to predict ecological effects, and provide fishery biologists with the quantitative foundation necessary to better manage stream salmonid invasions.

Cutthroat Trout

Behnke (1992) described the native inland trout of western North America and recognized 15 subspecies of cutthroat trout. Two of these subspecies, westslope cutthroat trout (*Oncorhynchus clarkii lewisi*; WCT) and Yellowstone cutthroat trout (*O. c. bouvieri*; YCT), occur in Montana and are the focus of this research. WCT historically occupied the broadest range of any cutthroat trout subspecies. The historical range of WCT was a contiguous area encompassing the upper Missouri, upper Columbia (including the upper Salmon, upper Kootenai, upper

Westslope cutthroat trout (*photo by D. Pearson, MSU*)

Yellowstone cutthroat trout (*photo by D. Pearson, MSU*)

Pend Oreille, and entire Clark Fork basins), and upper South Saskatchewan river basins, and several disjunct populations in the states of Washington and Oregon (Behnke 1992; Shepard et al. 2005). YCT historically occupied the upper Yellowstone and upper Snake River basins (Behnke 1992 and May et al. 2003).

The abundance and distribution of WCT and YCT have declined from historical levels throughout their range (Hadley 1984; Liknes and Graham 1988; Varley and Gressell 1988; Behnke 1992; McIntyre and Rieman 1995; Gresswell 1995; Van Eimeren 1996; Shepard et al. 1997; Kruse et al. 2000; May et al. 2003; Shepard et al. 2005; Meyer et al. 2006). Factors associated with this decline include introductions of nonnative fishes, habitat changes, and over-exploitation (Hanzel 1959; Liknes and Graham 1988; Behnke 1992; McIntyre and Rieman 1995). WCT and YCT populations have been displaced from many of their historical habitats by nonnative trout (Shepard et al. 1997; May et al. 2003; May 2007). While WCT appear especially sensitive to displacement in larger streams and rivers, and now often persist only in isolated headwater refuges, especially in the Missouri River basin (Shepard et al. 1997), YCT may be more resistant to displacement in larger rivers (May et al. 2003; DeRito 2004; May 2007). Brook trout *Salvelinus fontinalis* now occupy many of the headwater habitats previously occupied by cutthroat trout (Behnke 1992; McIntyre and Rieman 1995) and continue to invade and displace populations of native cutthroat trout (MacPhee 1966; Griffith 1972; Behnke 1979; Liknes and Graham 1988; Griffith 1988; Dunham et al. 2003).

The term “replacement” has been used when one species declines, often due to habitat degradation, and another species subsequently invades and replaces them (Griffith 1972; Griffith 1988; Dunham et al. 2003). The term “displacement” indicates that one species out-competes or preys upon another species and eventually displace them from suitable habitats. Replacement and displacement have both been suggested as mechanisms leading to brook trout predominating streams once dominated by cutthroat trout subspecies (Griffith 1972; Behnke 1979; several papers in Gresswell 1988; Krueger and May 1991). Griffith (1988) reviewed the available literature and could not determine whether declines and extirpation of cutthroat trout from many of their historically occupied habitats by nonnative salmonids was due to competitive exclusion (displacement) or replacement following changes in habitat quality.

Cutthroat trout evolved under diverse conditions resulting in a high level of genetic and life history variability both among and within the subspecies (Shepard et al. 1984; Allendorf and Leary 1988; Gresswell 1997; Taylor et al. 2003; Wofford et al. 2005; Cegelski et al. 2006). The different life histories exhibited by cutthroat trout and estimates of their demographic rates have been widely reported (Miller 1953; Irving 1954; Ball and Cope 1961; Johnson 1963; Brown 1971; Behnke 1972; Lukens 1978; Gresswell 1980; Shepard et al. 1984; Bjornn and Liknes 1986; Liknes and Graham 1988; Varley and Gresswell 1988; Rieman and Apperson 1989; Bjornn and Reiser 1991; Downs et al. 1997; Meyer et al. 2003). For this research WE studied “resident” forms of WCT and YCT that remain in their natal tributaries through maturity. For this review we focused on a few demographic rates that we believe are critical in determining the outcomes of species interactions between brook and cutthroat trout.

We concentrated on spawning and emergence timing, fecundities, early survival, growth, food habits, and age or size at maturation (Table 1). We also reviewed habitat use, especially spawning habitat, habitat preference during the first year of life, use of cover, thermal preferences, and thermal limits for these species (Table 2).

Brook Trout

The natural historical range of brook trout extends from the Saskatchewan River to Hudson Bay and Labrador in Canada southward along the Appalachian Mountains to the state of Georgia and west to the upper Mississippi River system (Brown 1971). Brook trout have been widely stocked by fish management agencies throughout the western United States and are one of the most widespread nonnative species in this region (Fuller et al. 1999; Dunham et al. 2002a). Brook trout were widely stocked in Montana from their first introduction in to the Yellowstone River drainage in 1889 until 1954, when stocking was sharply reduced (Brown 1971; Figure 1). By 1970 Brown (1971) indicated that brook trout inhabited almost all Montana counties with waters suitable for trout.

Brook trout (*photo by D. Pearson, MSU*)

Brook trout, like cutthroat trout, also have diverse life history strategies and high within-species variability (Power 1980; Angers et al. 1995; Dunham et al. 2002a), probably due to the diverse conditions under which they evolved. Brook trout have the ability to disperse both upstream and downstream to colonize suitable habitats (Smith and Saunders 1958; Flick and Webster 1975; Erman 1986; Riley et al. 1992; Gowan and Fausch 1996; Adams 1999; Adams et al. 2000; Adams et al. 2001; Rodriguez 2002; Adams et al. 2002; Peterson and Fausch 2003; Petty et al. 2005; Roghair 2005). The exploratory migratory behavior exhibited by brook trout may have its evolutionary roots in the close association this species had with the continental ice sheets and their need to disperse during expansion and recession of these glacial ice sheets (Power 2002), a factor that also probably contributed to the migratory behavior of many northern Rocky Mountain cutthroat subspecies like WCT and YCT. Invasion of brook trout, *Salvelinus fontinalis*, into habitats occupied by native cutthroat trout, *Oncorhychus clarkii*, offers an opportunity to study invasion ecology in the Northern Rocky Mountains of the western U.S. (Dunham et al. 2002a).

Brook Trout Invasion

For invasion to be successful individuals must not only be able to disperse, but habitats to which they disperse must be capable of supporting a reproducing population (Adams 1999; Dunham et al. 2002a; Kennedy et al. 2003; Benjamin 2006; Benjamin et al.

2007). Brook trout appear to have flexible life histories that allow them to successfully inhabit both warmer, low elevation sites and colder, infertile, high elevation sites (Kennedy et al. 2003). Unconfined valley bottoms, especially those that contain beaver ponds, may act as refuges and sources for brook trout invasion (Benjamin 2006; Benjamin et al. 2007). While beaver dams can restrict or prevent upstream movement, beaver ponds can provide moderate temperatures, cover, and food resources important for brook trout (Rupp 1954; Allen and Claussen 1960; Winkle et al. 1990; Johnson et al. 1992; McRae and Edwards 1994; Collen and Gibson 2001). Collen and Gibson (2001) indicated that brook trout are better adapted to pond conditions than many other salmonid species and that brook trout dominated Atlantic salmon (*Salmo salar*) in streams with beaver ponds. Beaver ponds may be particularly important as winter habitat and several studies have indicated that both brook and cutthroat trout prefer beaver ponds during the winter (Jakober et al. 1998; Lindstrom and Hubert 2004).

Nonnative brook trout *Salvelinus fontinalis* have successfully invaded and now occupy many of the headwater habitats previously occupied by cutthroat trout, often leading to declines or extinction of cutthroat trout populations (MacPhee 1966; Griffith 1972; Behnke 1992; several papers in Gresswell 1988; Krueger and May 1991; McIntyre and Rieman 1995; Shepard et al. 1997; Dunham et al. 2002a). Griffith (1988) reviewed the available literature and could not determine whether observed declines and extinctions of cutthroat trout populations following invasion by nonnative salmonids was due to competitive exclusion (displacement) or replacement following changes in habitat quality. WCT appear especially sensitive to replacement or displacement in larger streams and rivers, and now often persist only in isolated headwater refuges, especially in the Missouri River basin (Shepard et al. 1997).

Dunham et al.'s (2002a) review of the effects of brook trout on cutthroat trout found that competition, predation, and parasite or disease transmission were the three most commonly cited mechanisms for displacement of cutthroat by brook trout. McGrath and Lewis (2007) concluded that predation by brook trout on greenback cutthroat trout (*O. c. stomias*) was too low to account for displacement of cutthroat trout by brook trout based on analyses of stomach contents and stable isotopes. Competition appears to be a more likely mechanism for displacement of cutthroat trout by brook trout and many researchers have suggested that this competition likely occurs at young ages, but few studies have explicitly tested this speculation (Novinger 2000; Shepard et al. 2002; Peterson et al. 2004; Hilderbrand 2003; McGrath and Lewis 2007).

Crowder (1990) suggested the most rigorous evidence to demonstrate competitive interactions could be gained by showing "repeated changes in growth or abundance when resource levels or competitors are manipulated experimentally." Peterson and Fausch (2003) presented a conceptual framework for a manipulative field experiment to test for population-level mechanisms causing ecological effects and promoting invasion success by isolating segments of streams with different physical characteristics and physically removing the invasive species to document the response of the native species. They suggested that experiments of this type could provide invasion ecologists a useful example of how a taxon-specific invasion framework can improve the ability to predict ecological effects, and provide fishery biologists with the quantitative foundation necessary to better manage stream salmonid invasions. They applied this technique in relatively short segments (0.8 and 1.2 km) of two streams where they removed brook trout and assessed the response of cutthroat trout over three years (Peterson and Fausch 2004).

Competition and Predation

Underwater photo of Yellowstone cutthroat trout (*photo by D. Pearson, MSU*)

Both competition and predation have been suggested as potential mechanisms by which brook trout displace cutthroat trout (Dunham et al. 2002a, 2004). Competition has been shown as a likely mechanism by which brook trout displace cutthroat trout in numerous studies (Fausch 1988; Griffith 1988; Adams et al. 2000; Dunham et al. 2002a; McGrath and Lewis 2007); however, few studies have investigated competition between wild fish in the field and most of these studies used indirect measures (i.e. food habits; Griffith 1972, 1974; Cummings 1987; Schroeter 1998; Dunham et al. 2000; Peterson et al. 2004; McGrath and Lewis 2007). Competition can only be demonstrated by measuring a niche shift or a reduction in abundance, density, or body condition of one or both species in sympatry compared to allopatry (e.g. Nilsson 1967; Ross 1986).

Brook trout spawn in the fall, their embryos incubate through the winter, and their fry emerge during the late spring to early-summer period, while cutthroat trout spawn in the early summer, usually after peak snowmelt runoff, their embryos incubate during the summer, and their fry emerge during late summer or fall. This differential in emergence timing provides age-0 brook trout with a 20 to 25 mm size advantage over age-0 cutthroat trout, at least through their first year of life (Griffith 1972; Novinger 2000). Food habits studies have demonstrated considerable dietary overlap between brook and westslope cutthroat trout, but authors of these studies concluded that brook trout did not limit food for cutthroat trout (Griffith 1974; Dunham et al. 2000; Hilderbrand and Kershner 2004; McGrath and Lewis 2007). While Griffith (1972) found that same age brook trout consistently dominated cutthroat trout in laboratory experiments due to their larger size, he observed that in a natural stream the two species used different microhabitats, a finding Novinger (2000) confirmed in a later study. However, Griffith later (1974) reported that neither food nor habitat preferences differed much between age-0 brook and westslope cutthroat trout inhabiting four Idaho streams, whether they lived in sympatry or allopatry.

Cummings (1987) and Thomas (1996) both suggested that competition between brook and cutthroat trout likely occurred at young ages. Underwater microhabitat observations on positions occupied by brook trout and greenback cutthroat trout, *O. c.*

stomias, by Cummings (1987) indicated that juvenile brook trout excluded juvenile cutthroat trout from “more profitable” stream positions. Thomas (1996) observed that young brook trout inhibited the foraging efficiency of juvenile Colorado River cutthroat trout. She suggested this inhibition might be the mechanism responsible for decreased growth rates in cutthroat trout she documented. She also reported a reduction in lipid reserves in young cutthroat trout exposed to competition with brook trout. McGrath (2004) and McGrath and Lewis (2007) found that brook trout displaced greenback cutthroat trout in sites where the species occurred together in Colorado. She suggested that competition for food among adult trout of these two species is not a major mechanism for displacement of greenback cutthroat trout by brook trout and hypothesized that the major effect of brook trout are on age-0 cutthroat trout, but was uncertain of the exact mechanism (McGrath and Lewis 2007).

Shepard et al. (2003) also hypothesized that the major effect of brook trout was on age-0 WCT based on the dramatic rebound of age-0 WCT following removal of brook trout from a Montana stream. Peterson and Fausch (2004) tested effects of brook trout on Colorado River cutthroat trout *O. c. pleuriticus* in experimental sections of four Colorado streams by experimentally removing brook trout from two sections. Their study documented that brook trout reduced the survival of young cutthroat trout. Sensitivity and elasticity analyses for stage-structured cutthroat trout population models indicated that survivals for early life stages (young-of-the-year and juveniles) had the most effect on population growth rate (Stapp and Hayward 2002; Hilderbrand 2003), a finding we have independently verified.

While predation by brook trout on cutthroat trout has been suggested as a potential mechanism for displacement, little direct evidence exists to suggest predation is a major factor. Much of the evidence for predation of brook trout upon cutthroat trout was based on field enclosure experiments, where brook trout were either found or suspected of preying on cutthroat trout within the enclosures (Gregory and Griffith 2000; Novinger 2000). Food habits studies in open stream systems have found fish prey in very low proportions within either brook or cutthroat trout stomachs (Griffith 1970; Dunham et al. 2000; McGrath and Lewis 2007). McGrath (2004) investigated the relative position of greenback cutthroat trout and brook trout within the food web using stable isotope analyses and found that these species functioned similarly in their transfer of energy within the food web. From this stable isotope analysis and her calculated predation rates she concluded that predation by brook trout on cutthroat trout was not a major factor in the displacement of cutthroat trout by brook trout.

Habitat

Relationships between salmonid abundance and habitat variables have been studied and modeled in many studies (see Fausch et al. 1988 and Rosenfeld 2003 for reviews). Stream habitats are hierarchical (e.g. Frissell et al. 1986; Hawkins et al. 1993; Rosenfeld 2003). While Rosenfeld (2003) cautioned against using associations between habitat variables and species occurrence, or abundance, in the wild to infer habitat requirements for a particular species, he contends that his research on juvenile cutthroat trout has shown that habitat use and selection in the wild are congruent with the fitness consequences of habitat use for this species (Rosenfeld et al. 2000; Rosenfeld and Boss 2001). Rosenfeld et al. (2000) indicated that cutthroat trout occupied smaller stream channels (estimated using bank-full channel width) with adult cutthroat trout preferring pool habitats. Rosenfeld and Boss (2001) showed that pool habitats provided higher growth rates to both juvenile and adult cutthroat trout than riffle habitats.

Platts (1979) identified relationships between habitat variables estimated at a large-scale and abundance of several species of salmonids and reported longitudinal gradients among species. Franco and Budy (2005) also reported a longitudinal gradient where Bonneville cutthroat trout (*O. c. utah*) inhabited the headwater reaches and brown trout (*Salmo trutta*) inhabited the lower reaches of the Logan River drainage, Utah. Franco and Budy (2005) found a transition zone between these two species that supported relatively low trout densities and that cutthroat abundance was affected by diel water temperatures and the presence of brown trout, while brown trout abundance was affected by discharge and the presence of cutthroat trout. Binns and Remmick (1994) found that abundance of Bonneville cutthroat trout in Huff Creek, Wyoming was correlated to the previous year's stream discharge, the quantity of cover, and pool area. Nelson et al. (1992) related the distribution of Lahontan cutthroat trout (*O. c. henshawi*) and their habitats to the geology and geomorphology of the North Fork Humboldt River basin in Nevada. Bozek and Hubert (1992) assessed relationships between climate, stream energy, and stream size on presence and absence of cutthroat, brook, brown, and rainbow trout in the central Rocky Mountains. They were able to successfully predict the presence of brook trout for 87%, cutthroat trout for 59%, brown trout for 50%, and rainbow trout for 39% of their sampled sites; however, they were better able to predict the absence of these four species.

Fausch (1989) suggested that distributions of brook and cutthroat trout might be influenced by stream gradient. He suggested that brook trout occupied lower gradient stream reaches (with maximum abundance observed at gradients less than 3%), while westslope cutthroat trout occupied primarily higher gradient reaches (with maximum abundance in gradients ranging from 6 to 14%). He suggested three potential mechanisms that may limit brook trout distribution and abundance in higher gradient stream reaches. First, brook trout may be poorer swimmers than cutthroat trout, so cannot ascend into higher gradient reaches. Second, brook trout have not had enough time since their introduction to invade all the available higher gradient headwater portions of streams. Finally, reproduction and recruitment of brook trout in high gradient stream reaches may be limited due to lack of groundwater up-welling areas and lack of slow water rearing habitats for young of the year brook trout, especially during the late spring and early summer immediately after brook trout fry emerge and high snowmelt runoff usually occurs.

Shepard et al. (1998) developed a multiple regression model that indicated that the presence and abundance of brook trout overrode effects of habitat on densities of westslope cutthroat trout (physical effects model R^2 = 0.04; physical effects plus brook trout effects model $R^2 = 0.67$). We found significant interactions between brook abundance and several habitat components (temperature and land use) that affected densities of cutthroat trout. We also reported that brook trout dominated a stream that had higher summer water temperature, more woody debris, and higher proportions of fine in the streambed and pool habitats than two adjacent streams where WCT dominated (Shepard 2004).

Temperature

Water temperature is a major factor controlling growth in fish (Weatherly and Rogers 1978; Donald et al. 1980; Stewart and Binkowski 1986; Beauchamp et al. 1989; Fechhelm et al. 1992; Johnson et al. 1992; Weatherley et al. 1991; Van Winkle et al. 1997; Hayes et al. 2000; Nislow et al. 2000; Stoneman and Jones 2000; Forseth et al. 2001; Ojanguren et al. 2001). Many studies have demonstrated that water temperature may influence the distribution and/or abundance of brook and cutthroat trout (Burton and Odum 1945; MacCrimmon and Campbell 1969; Vincent and Miller 1969; Meisner 1990a and 1990b; Nelson et al. 1992; Paul and Post 2001; Benjamin et al. 2007). Several studies have implied that brook trout may perform better than cutthroat trout at warmer (> 15 C) water temperatures (De Staso and Rahel 1994; Dunham et al. 1999; Novinger 2000). DeStaso and Rahel (1994) conducted laboratory micro-habitat studies between brook and greenback cutthroat trout, *O. c. stomias*, at two different water temperatures and observed that brook trout showed a clear competitive dominance over cutthroat trout at water temperatures of 20 C versus 10 C.

Taniguchi and Nakano (2000) suggested that temperature-mediated condition-specific competition between *Salvelinus malma* and *S. luecomaenis* partly explained the altitudinal distribution differences between these two species in streams of Japan. While they elegantly demonstrated differences in behavioral dominance, food intake, and growth for these two species at warmer temperatures, they could not explain why *S. malma* existed in allopatry in higher elevation colder reaches when neither species clearly dominated in laboratory trials at lower temperatures. They hypothesized that the higher survival rates they observed for *S. malma* at the colder temperatures in their laboratory trials, though inconsistent with the lower food acquisition and growth rates they measured, may have been a species-specific physiological trait of starvation resistance in *S. malma*. Taniguchi and Nakano did not explicitly consider other environmental variables as potentially influencing the distribution of these two species, but mentioned that a single variable may not always accurately predict a community pattern. Temperature likely influences the distribution of brook trout and their interactions with cutthroat trout in subtle and complex ways that are not fully understood (Dunham et al. 2003).

Habitat Restoration

Marchetti et al. (2004) suggested that restoration of natural hydrologic processes might reduce invasion impacts based on a study of fish invasion in California, USA. Design criteria used for restoring stream channels must account for the natural processes that form and maintain each individual stream reach (Kondolf et al. 2001). Habitat restoration sometimes is implemented at the watershed scale, but more often occurs at the stream reach or stream section scale. Roni et al. (2005) reviewed previous evaluations of instream enhancement and found most evaluations focused on the responses of the physical habitat. They also found that where response of fish was evaluated, trout species were most frequently the species evaluated.

Binns and Remmick (1994) assessed the effects of 68 instream habitat structures, rock riprap, and improved livestock management using exclosures and herding on Bonneville cutthroat trout (*O. c. utah*) in Huff Creek, Wyoming. They found that cutthroat trout densities and standing crops were highest within an exclosure that also contained instream structures. Pools that were created by instream structures were deeper than natural pools. Binns (1999) reviewed the response of trout to 71 different projects in Wyoming and detected increases in trout abundance either after treatments or between treatment and control reaches. However, most projects reviewed by Binns had few years of data collection and confounding factors such as fencing livestock off of stream channels or complete removal of livestock grazing that made it difficult to attribute the response detected in trout abundance to a specific management action. Barrineau et al. (2005) evaluated winter habitat for cutthroat and book trout created by instream pool structures in a low gradient stream of Wyoming. They found that the presence or absence of nearby groundwater affected the instream structures and use of pools by trout.

The distributions and abundances of native westslope and Yellowstone (*Oncorhynchus clarkii lewisi* and *O. c. bouvieri*) cutthroat trout in the Northern Rocky Mountain region have declined from historical levels, and both subspecies are considered at risk for listing under the Endangered Species Act. Efforts are currently underway to conserve these subspecies throughout the region. One important conservation strategy is that of habitat restoration and enhancement, but few studies have quantitatively assessed the responses of cutthroat trout populations following habitat restoration. In fact, few studies have described what constitutes ideal habitat for these subspecies, making restoration imprecise and unpredictable. In addition, competition and predation by non-native trout species, particularly brook trout that frequently occur in sympatry with both subspecies, is another major threat to their conservation. Interactions between brook and cutthroat trout are likely regulated by habitat condition, but little is known about these relationships.

Goal and Objectives

The goal of this project was to identify habitat conditions that promote the continued persistence of westslope and Yellowstone cutthroat trout in the Northern Rocky Mountains. Specific objectives were to: (1) determine if nonnative brook trout and native cutthroat trout occupy similar habitat niches in Northern Rocky Mountain headwater tributaries; (2) illustrate whether stream habitat restoration strategies commonly used in Montana are effective in increasing abundance of cutthroat trout; (3) evaluate how habitat condition interacts with brook trout presence and abundance to affect the abundance and distribution of cutthroat trout; and (4) assess the effect of presence of non-native fishes on success of cutthroat trout habitat restoration projects. We also investigated whether (1) nonnative brook trout and native cutthroat trout consumed the same prey items during the summer and (2) age-0 brook trout and cutthroat trout compete with each other prior to entering their first winter. This project was a collaborative effort between Montana Fish, Wildlife & Parks, the Montana Cooperative Fishery Research Unit, and Montana State University. In addition to SWIG funding, funding was also provided by the Wild Fish Habitat Initiative through the Montana Water Center.

Study Area

We sampled cutthroat and brook trout populations and habitats in the Northern Rocky Mountains of Montana (Figure 1). We sampled over 1,000 sample sites (Figure 1). Water temperature data were collected from a number of sampled streams.

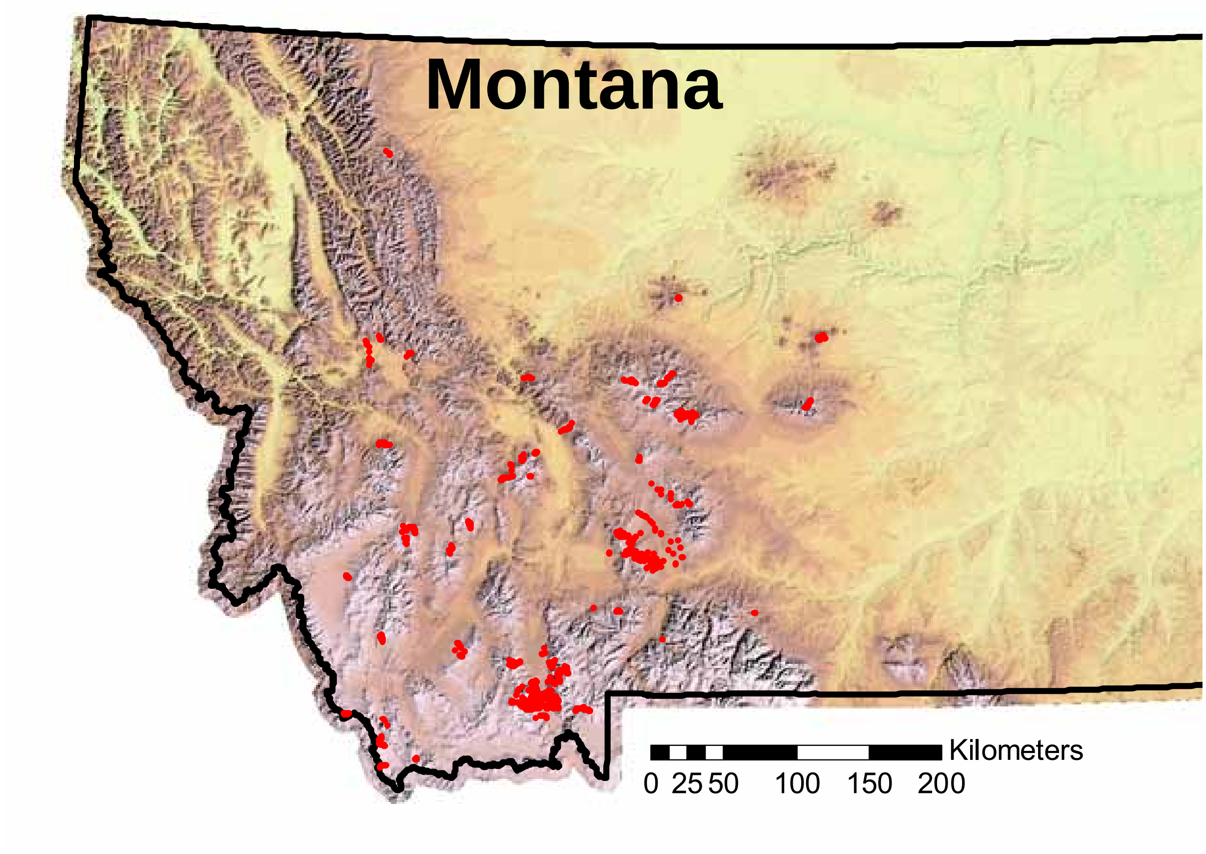
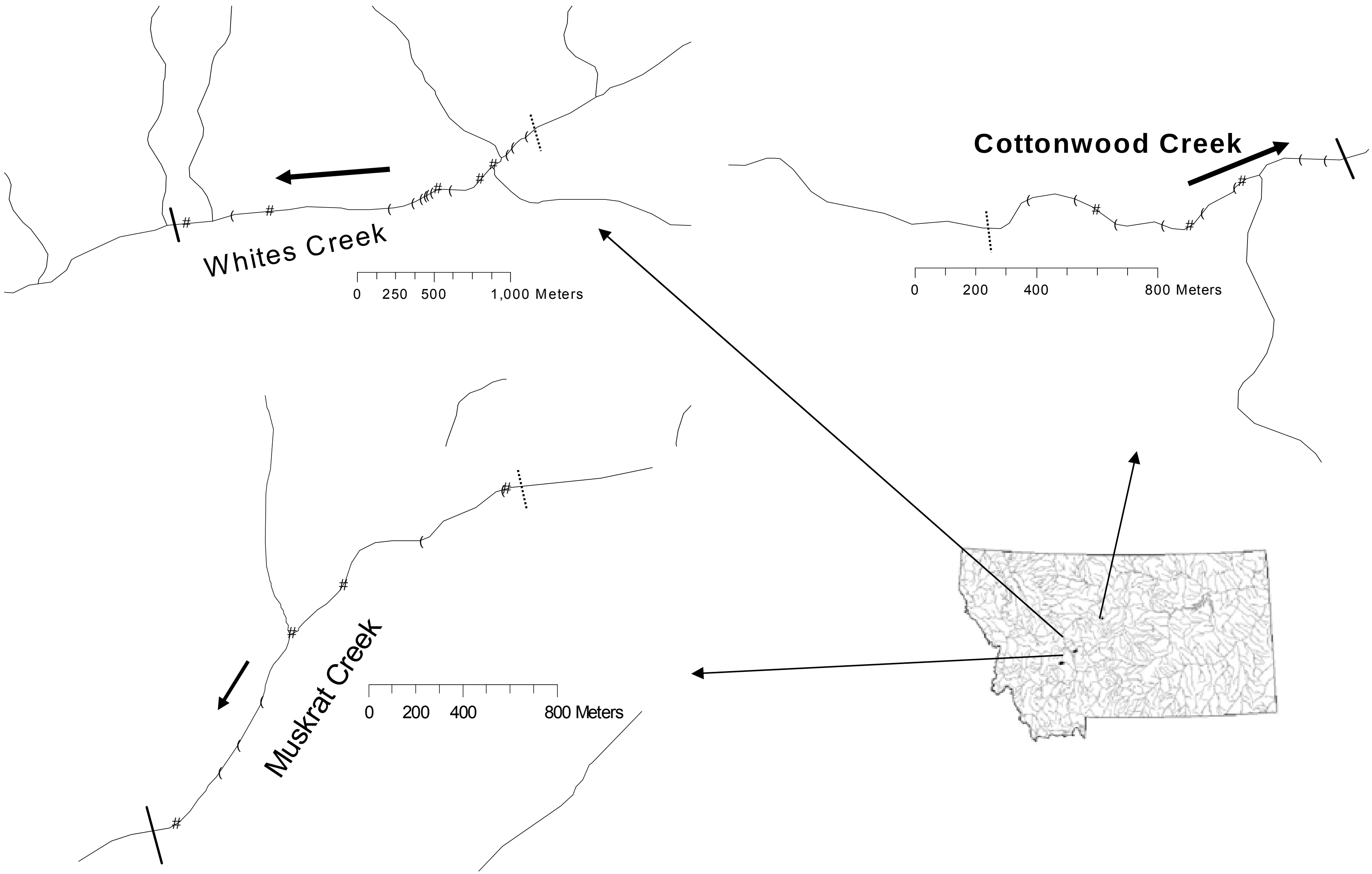


Figure 1. Map of the western two-thirds of Montana showing all sites (red dots) sampled from 1993 through 2007.

To evaluate whether niches occupied by cutthroat trout and brook trout were similar, we removed brook trout from 2.3 to 3.0 km reaches in Cottonwood, Muskrat, and Whites creeks, located within the upper Missouri River basin in Montana (Figure 2). These streams were relatively small, cold, neutral to alkaline, and unproductive (Table 1). The only fish species present within all study reaches were WCT and brook trout. Invasion by brook trout in Cottonwood Creek appeared to be relatively recent as brook trout were present in moderate densities at the lower end of the treatment reach, rare in the middle portion of the treatment reach and absent from

Figure 2. Map of brook trout removal study streams showing their location in Montana, lower boundary barriers, extents of brook trout removal treatments, and locations of sample sections within treatment reaches.



the uppermost portion of the stream. Conversely, brook trout were well established throughout treatment reaches in Muskrat and Whites creeks.

Table 1. Physical characteristics of three Rocky Mountain streams where westslope cutthroat trout response to brook trout removals was evaluated from 1993 through 2007.

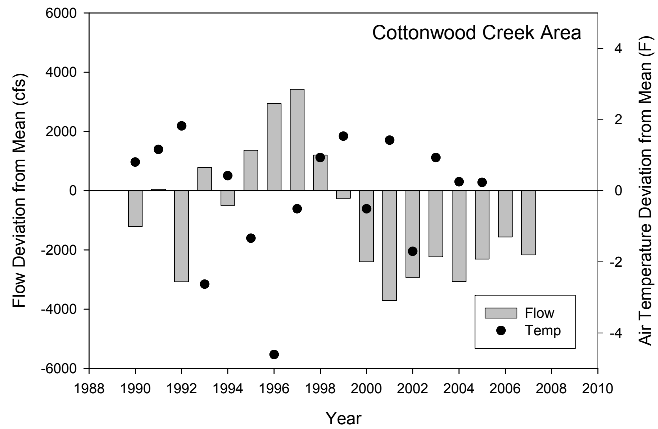
	Stream		
Parameter	Cottonwood	Muskrat	White's
Elevation range of entire stream (m)	970-1830	1480-2350	1200-1870
Elevation range of treatment reach (m)	1590-1780	1920-2110	1600-1790
Length of stream (km)	31.1	33.9	25.5
Treatment length (km)	3.0	2.3	2.9
Wetted width (m)	2.4	2.6	2.0
Channel order[1/]	3rd	3rd	3rd
Channel gradient (%)	6	6	3
Riparian vegetation (density and predominant types)	Sparse willow, aspen	Moderate conifer, alder	Moderate willow, alder
Late summer flow (m^3/sec)	0.10	0.17	0.08
Summer water temperature (C)	12-17	6-16	8-10
Conductivity (μmhos)	88	72	660
PH	8.7	8.4	8.2

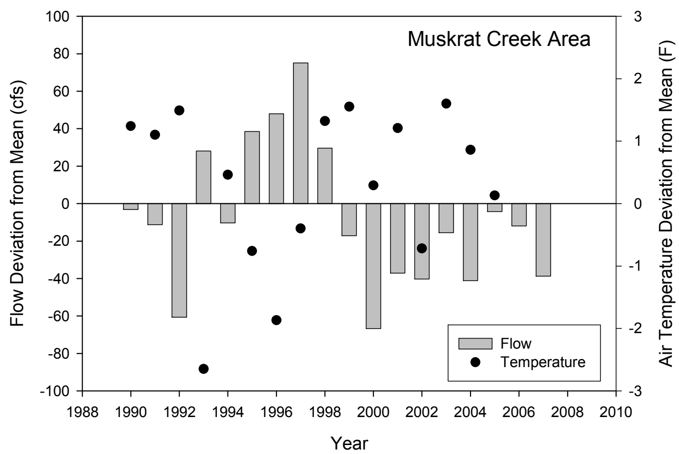
[1/] Strahler (1957) stream order.

Barriers to upstream fish movement were constructed at the lower boundary of each treatment reach. Two barriers were wooden crib barriers and one was a cement barrier faced with rock. Barriers had 1.5 to 3.0 m vertical drops and impervious splash pads to prevent plunge pools from forming below the barrier. Testing of these barriers using marked fish placed below the barriers confirmed that these barriers prevented upstream invasion by nonnative fish. We monitored four or five sample sections within each brook trout eradication reach during and following brook trout eradication (Figure 2). In Muskrat Creek a natural barrier located at the top of the treatment reach prevented upstream movement of fish. Above this barrier Muskrat Creek did not support any fish prior to 1997 when we began moving some WCT from the treatment reach above this natural barrier to expand their distribution within this stream.

Wooden crib barrier when first installed in Whites Creek (*photo by R. Spoon, FWP*)

Stream and river flows in the upper Missouri basin were near average in the early 1990's, above average in the late 1990's, much below average in the early 2000's, and slightly below average in the mid-2000's (Figure 3). Average annual air temperatures generally followed an inverse pattern to flows (Figure 3).





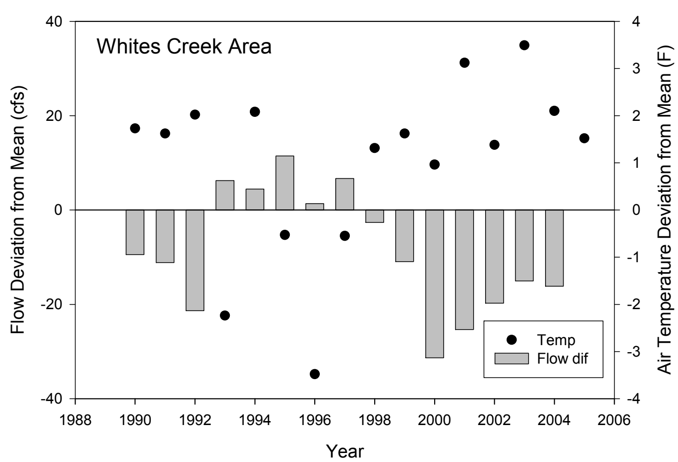


Figure 3. Annual flow and temperature deviations from long-term means from 1990 through 2007 for sites near sample streams.

A comparative food habits study was also conducted in White's and Muskrat creeks (Figure 2). Fish barriers were constructed in White's Creek in 1994 and Muskrat Creek in 1997. All brook trout were removed using repeated electrofishing from these streams above the fish barriers from 1993 through 2000 in Whites Creek and from 1996 through 2004 in Muskrat Creek. We found no evidence of brook trout above constructed fish barriers in either stream following successful brook trout eradication during this study.

Methods

Field methods that were common to most of the studies are presented first, and then methods specific to each study are detailed later.

Fish were captured using Smith-Root® BP-15, BP-12, and SR-24 model backpack shockers operated at voltages in the range of 100 to 600 V, frequencies under 50 Hz, and pulse widths less than 2 μsec to maximize the number of fish captured, while minimizing injury to fish caused by shocking (Dwyer et al. 2001). An electrofishing crew consisted of either two or three people. One crewmember wore the backpack shocker and shocked using a wand anode while dragging a cable cathode. A second crewmember was the primary dip netter who followed the shocker netting all stunned fish. When a third crewmember was available, this person held a dip net in the stream channel below the two other crewmembers and carried a mesh bucket for transporting captured fish. Either block nets or fencing material (6.5 mm mesh) were installed at sample section boundaries, or boundaries of sample sections had natural breaks that limited fish movement into or out of sample sections during sampling.

L. Renner and D. Pearson with electrofishing gear (*photo by B. Shepard, FWP*)

D. Staples and L. Renner installing a block net (*photo by B. Shepard, FWP*)

Electrofishing passes were generally conducted within four hours of each other.

The assumption of population closure was met by: 1) using either block fences or nets at the upper and lower ends of sample sections or locating sections so they had shallow riffles or velocity barriers at their upper and lower boundaries; 2) using a second netter during most sampling to prevent fish from moving downstream; and 3) the relatively short time it took to complete all sample passes (White et al. 1982).

Lengths (total length in mm), species, and pass number were recorded for all captured fish. Weights (g) were measured for almost all captured fish using battery-powered electronic scales (O'Haus® models CS and CL); however, during a few sampling events weights were not recorded due to equipment malfunctions. While scale accuracy was 0.1 g, all fish were weighed to the nearest gram.

Population estimates were calculated using depletion estimators (Van Deventer and Platts 1989) for fish 75 mm and longer. Depletion estimators consistently under-estimate true populations, especially when only two passes are made and capture probabilities are less than 0.90 (Riley and Fausch 1992). White et al. (1982) recommended that three or more passes be done unless the capture probability is 0.8 or higher. Riley and Fausch (1992) suggested that three passes reduced estimate bias and through simulation suggested that bias was extremely low at capture probabilities above 0.9 and relatively low at capture probabilities over 0.8. Capture probabilities for most of our two-pass estimates were 0.8 or higher. When no fish were captured on the second pass of a two-pass estimate, the total population was assumed to be the total number of fish captured on the first pass.

For each species we made depletion population estimates for all fish 75 mm and longer within each sampling section. Estimates of total standing crop (g/m^2) and density (number/ha) were made for each species for fish 75 mm and longer. We estimated total standing crops (g/m^2) for each sample section by year by summing estimated total weights divided by area sampled within each sample section. Density per section was derived by dividing the section estimates by the total area of each estimate section to derive the density per section.

We developed length-weight regression models for each species by stream and year and for each stream over all years sampled. Log_{10} transformations of both lengths and weights were used (Anderson and Gutreuter 1983). Since slopes of $\log_{10}$(length) to $\log_{10}$(weight) regressions were near 3.0 for almost all species and year combinations, we assumed isometric growth and computed Fulton-type condition factors as these were easier to compare among years within streams than were regression metrics (Pope and Kruse 2007). We computed the condition factor for each individual WCT for which both length and weight had been measured using the formula (Anderson and Gutreuter 1983):

$$K = \frac{100{,}000 * W}{L^3}; \qquad \textit{[eq. 1]}$$

where K = condition, W = weight (g), and L = length (mm).

We estimated various habitat parameters at two scales (site and watershed) by measuring habitat variables at sample sites in the field and using a geographic information database (ArcGIS 9, version 9.2; ESRI 1999-2006; www.esri.com). Field habitat surveys estimated the following parameters from 1992 to 2007 within most sample sections (termed "sites") where fish population estimates were made:

1. length (m), wetted width (m), total number and proportion of each macro-habitat type (classified as pool, riffle, or run);
2. average pool depth and average pool thalweg depth (cm), and residual pool volume (computed by measuring residual depth as defined by Lisle [1987] and multiplying residual depth times surface area);
3. surface area of suitable spawning habitat (defined as patches of substrate dominated by material 1 to 3 cm diameter comprising at least 0.3 m^2 of the streambed's surface);
4. number of large ($\geq$15 cm diameter) and small (<15 cm) woody debris within and across the wetted stream channel;
5. qualitative assessments (ranked from low = 1 to high = 10) of stream bank condition, instream cover, bank overhead cover, and land use impacts within riparian areas;
6. percentage of surficial substrate material in boulder, cobble, large gravel, small gravel, sand, and silt; and
7. temperature, conductivity, and pH were measured over several sample periods and averaged.

We deployed Onset Optic Stowaway recording thermographs in many of the streams during the summer season (middle of June through September). These thermographs recorded water temperatures at 0.5-hour intervals. These data were brought into a Microsoft Access database and we summarized daily mean, minimum, and maximum temperatures.

Response of Westslope Cutthroat Trout to Removal of Brook Trout

To document whether nonnative brook trout occupied a similar niche as native westslope cutthroat trout we assessed how cutthroat trout responded after removal of brook trout in three relatively long stream reaches. Montana Fish, Wildlife, and Parks led several collaborative efforts to eradicate brook trout from portions of several streams from 1993 through 2003 (Shepard et al., *in review*). Total barriers to upstream fish movement were constructed at the lower bound of each treatment reach. Eradication efforts were successful in the treatment reaches of four streams, and eradication required three to seven years of at least annual removal efforts. In three of these streams monitoring of several sample sections within each of the 2.3 to 3.0 km long eradication reaches has occurred for at least three years following eradication to evaluate the response of WCT following the eradication of brook trout. We compared estimates and variances of standing crops (g/m^2) for each species ($\geq$ 75 mm; TL) in sympatry, prior to brook trout eradication, and for WCT in allopatry, following brook trout eradication, to evaluate whether brook trout occupied a similar niche as WCT in these study streams. We compared estimated length-weight condition factors for juvenile and adult WCT to estimated densities of juvenile and adult WCT and brook trout to determine whether inter-specific or intra-specific competition was influencing body condition of WCT. We compared densities of juvenile WCT to densities of juvenile and adult densities of brook trout and adult WCT to determine how observed changes in juvenile densities of WCT were related to brook trout removal efforts. We provide interpretation of observed changes to infer possible effects of brook trout on WCT.

We used electrofishing to remove brook trout and estimate populations of brook trout and WCT using depletion estimators (Van Deventer and Platts 1989). Brook trout were successfully eradicated from treatment reaches in Whites Creek in 2000 and in Cottonwood and Muskrat creeks in 2003 (Shepard and Nelson *in preparation*). Population and biomass estimates for each species 75 mm and longer were conducted prior to, during, and following electrofishing removal of brook trout.

Sampling was generally conducted from late July through early October. A few sample events occurred in late October and some movement of fish to winter habitats had likely occurred before these late sampling events. Most sample sections were 100 to 200 m in length. During initial brook trout removal efforts a couple (two sample events) sample sections were subdivided and when that was the case we pooled those subdivided sections to match later sample section length. Conversely, we infrequently (six sample events) sampled much longer sections during removal efforts. While these occasional deviations from consistent sample section boundaries might have affected our results, we assumed that converting our estimates to estimated weight or number per area for each sample event minimized this effect.

Of the 107 removal estimates we made, 82 were two-pass estimates, 24 were three-pass estimates, and 1 was a four-pass estimate. About 75% of all two-pass estimates had estimated probabilities of capture 0.8 or higher. There were four instances where fish numbers could not be estimated due to non-declining captures, two for brook trout (either one or two fish captured during each pass) in Whites Creek and two for WCT (three fish captured during each pass in one case and one fish captured in pass 1 and three fish captured in pass 2) in Muskrat Creek. For these cases we used the total weight of captured fish as the estimated standing crop for that species during that sampling event. While this protocol led to a slight underestimation bias, we assumed this bias was negligible and relatively consistent.

We made estimates of the density (number/m^2) of juvenile and adult WCT and brook trout within the treatment reaches by averaging all estimates conducted in each reach during July through October during each year. For each species we made depletion population estimates for all fish 75 mm and longer within each estimate sampling section. We also computed the proportion of captured fish within each size class (juvenile: 75 to 149 mm and adult: $\geq$ 150 mm) in each estimate section. By multiplying the proportion in each size class to the total estimate we derived the estimated number by size class. Density per section was derived by dividing the section estimates by the total area of each estimate section to derive the density per section. These estimates were pooled over all sample sections within the treatment reaches by averaging across all sampling sections where estimates were made.

We conducted two analyses using fish condition. First, we averaged these condition factors within two size classes that we assigned as juveniles (75 to 149 mm) and adults ($\geq$ 150 mm). We only used WCT that were captured from July through October to reduce the influence of the weight of sex products in mature adults. We tested whether significant associations between these estimated condition factors and estimated densities of juvenile and adult cutthroat and brook trout existed.

Secondly, we assessed relative effects of both intra- and inter-specific competition and size-asymmetric competition within the two streams that brook trout had successfully invaded and become well established (Muskrat and Whites creeks) by investigating effects that density of each species by size had upon body condition of individual cutthroat trout. We used Roughgarden's (1979) competition function (p. 531):

$$\alpha(d) = \exp\left(\sigma_v^2 \kappa^2\right) \exp\left[\frac{-\frac{1}{2}\left(d + 2\sigma_v^2 \kappa\right)^2}{2\sigma_v^2}\right]; \qquad \textit{[eq. 2]}$$

where d = difference between ln(length) of individual fish and ln(length) of competing fish;

σ_v^2 = breadth of competition parameter; and

κ = asymmetry parameter.

This competition function was summed over the estimated densities of all fish 75 mm and longer that were present by size to obtain the potential total effect of all fish in the population. The size groups were 75 to 79 mm and then increments of 10 mm size groups from 80 to 299 mm for a total of 23 size groups. We partitioned total population estimates of fish 75 mm and longer into these 23 length groups based on the proportion of fish captured within each length group. We computed the condition factor for individual fish and the natural log of individual fish condition was our dependent variable.

Statistical Testing

All statistical testing used a significance level of $p < 0.05$, unless otherwise indicated. We used SYSTAT© (version 11, SYSTAT 2004; http://www.systat.com) to conduct initial data explorations and the "R" statistical program (R Development Core Team 2008) to conduct final analyses.

Effect of Brook Trout Densities on Cutthroat Trout Densities

We tested for associations between the densities of juveniles and adults of both species to assess how densities of juvenile WCT were related to densities of juvenile or adult brook trout or adult WCT and if these associations were significant. We tested for these associations in the two streams where brook trout had successfully invaded and become well established (Muskrat and Whites creeks).

Standing Crop Comparisons

We compared total estimated standing crops before and after brook trout removal to determine whether there were significant differences in total standing crops when brook trout and WCT were in sympatry versus for WCT in allopatry by looking for overlap in standard errors. We plotted estimated standing crops in stacked bar graphs to evaluate the relative contribution of each species and illustrate the response of WCT following the removal of brook trout.

Effects of Brook Trout on Cutthroat Trout Abundance and Condition

The distributions of average condition factor and juvenile and adult densities by species were examined. The distributions of average condition factor appeared normally distributed and tests for normality did not indicate a significant deviation from normality; however, the relatively low sample size (29, much under the recommended minimum of 40) made this test inconclusive. Distributions for juvenile and adult densities were highly skewed with many zero densities, especially for brook trout following their removal. We used a lognormal transformation of the estimated densities and added 0.0001 to estimate densities prior to transformation to avoid returning an undefined number by taking the natural log of zero. While this natural log transformation helped normalize the WCT density data, the brook trout density data still was skewed due to many zero values.

We tested for associations between estimated condition of WCT and densities of juvenile and adult brook trout and WCT using Spearman rank correlation tests to avoid problems with the assumption of normality. We then ran “best subsets” regression analyses with either average condition of each size class or density of juvenile WCT as the dependent variable and the estimated densities of WCT and brook trout within each size class as independent variables. We evaluated densities during the year condition factors and juvenile WCT densities were estimated and for the previous year conditions factors and juvenile WCT densities were estimated by lagging our estimated densities by one year. Based upon results from these best subsets analyses we selected a few candidate models and conducted least squares multiple regression upon these candidate models.

To test intra- versus inter-specific competition and the potential strength of size-asymmetric competition upon condition of individual WCT we used the non-linear regression model with mixed-effects package “nlme” (Pinhero et al. 2008) within the “R” statistical software (R Development Core Team 2008). The model we tested was:

$$\ln(\text{Condition}) = \text{Year} + a^*(\text{competition function for WCT}) + b^*(\text{competition function for brook trout}). \quad [eq. 3]$$

We tested models that allowed for the same or different coefficients for brook trout and WCT competition effects ("a" and "b" in the above model, eq. 3), similar or different breadths of size-competition for brook trout and WCT (σ^2 in the competition function, eq. 2), and no size-asymmetry of competition versus a predicted size-asymmetry of competition (κ in the competition function, eq. 2). Values for all these variables were estimated simultaneously by non-linear modeling that applied the competition function for each species within the non-linear regression equation. Year was treated as a random effect in all models.

Abiotic and Biotic Factors Effecting Cutthroat Trout

We have collected information on presence, relative abundance, and actual population densities of cutthroat and brook trout throughout the Northern Rocky Mountains of Montana (Figure 1). Data used in this study were collected from 1993 through 2007. Two sample designs were used. One selected study streams based on the presence, or likely presence, of westslope cutthroat trout. The second design selected relatively large drainage basins (Madison, Shields, and South Fork Judith) and all tributaries within these larger basins were sampled. A systematic sampling scheme was used that sampled the range of cutthroat trout within each stream. Systematic sampling occurred at frequencies of from 1.0 to 3.0 km. Potential sample sites were selected and then we either started at a sample site where we believed cutthroat trout occurred (design one) or at the lowermost site (design two). Systematic sampling continued upstream until we found no fish in at least one, and usually two, sample locations. For design one, we sampled downstream until we did not find any cutthroat trout in at least two locations. For many streams in design one, a physical barrier to upstream fish movement was present at the lowermost boundary of the sampled reach.

Evaluation of Habitat Restoration

We queried the Montana Department of Fish, Wildlife and Parks habitat restoration database for any project that was completed and had targeted either westslope or Yellowstone cutthroat trout (Appendix A). We also made email, phone, and personal contacts with as many Montana biologists as possible to determine where habitat restoration projects were planned in waters that supported cutthroat trout.

Debris habitat enhancement in Dugout Creek (*photo by B. Shepard, FWP*)

We evaluated the effects of habitat restoration on populations of cutthroat and brook trout by using before-after (BA; Hicks et al. 1991), control-treatment (CT), and before-after with control-treatment (BACT or sometimes referred to as before-after with control-impact, BACI) sample-design approaches (Roni 2005). It was necessary to use all of these approaches because many of the sites where habitat restoration projects occurred did not initially have either treatment-control designs or good before-treatment fish population information. We assessed whether habitat enhancement increased the densities, relative weight relationships, or both of cutthroat trout in the presence of brook trout. We also evaluated the relative effects of pool habitat enhancement and woody debris additions on the densities and relative weight relationships of cutthroat trout in the presence of brook trout.

We designed and implemented a study using a BATC design for three sites, one with WCT and two with YCT. For these three sites we asked that different habitat restoration treatments be implemented in randomly selected stream sections so we could test the effects of pool development with and without the addition of woody debris. We compared estimated densities (fish $\geq$ 75 mm) and average condition factors (fish >100 mm) of the two cutthroat trout subspecies (WCT or YCT) and brook trout in control and treatment sample sections and, where applicable, pre- and post-treatment.

Comparative Food Habitats

Stomach contents were collected from westslope cutthroat trout and brook trout and invertebrate drift was simultaneously collected in Whites and Muskat creeks during early August 2005. Contents of stomachs were collected using gastric lavage (Light et al. 1983). We designed the study to compare food habits of cutthroat trout in sympatry with brook trout (below fish barriers) to cutthroat trout in allopatry above the fish barriers. We tried to collect stomach contents from at least five fish in each of two size groups ($\leq$ 125 mm and > 125 mm) from both species in sympatry and for cutthroat trout in allopatry; however, it was difficult to obtain the targeted sample sizes, especially for the small-sized cutthroat trout. Where we could not collect five small cutthroat trout we chose to either sample additional brook trout or additional larger cutthroat, thus, we sampled 10 allopatric cutthroat trout, five sympatric cutthroat trout, and 16 sympatric brook trout in Whites Creek and 10 allopatric cutthroat trout, four sympatric cutthroat trout, and 15 sympatric brook trout in Muskrat Creek.

Potential food items available to fish were sampled using drift nets set for one hour intervals during the morning, mid-day, and evening in Whites Creek and during the morning and evening in Muskrat Creek both above and below the fish barriers in each stream (Table 5). A single drift net was wide enough

Drift sample net in Whites Creek (*photo by B. Shepard, FWP*) that it sampled almost the entire stream width in Whites Creek and upper Muskrat Creek, while two drift nets set adjacent to each other sampled almost the entire stream width in lower Muskrat Creek. These drift nets collected both surface and subsurface drift.

Food items from each stomach and drift sample were picked from the samples and identified to Order and Family (some were classified to Genus and species), counted, and weighed (wet weight) by Order and Family (or Genus or species, where possible). Keys to adult and immature insects were used to identify food and drift organisms. When organisms were partially digested or broken up, an attempt was made to count heads of identifiable organisms. When items could not be identified they were classified as such. Our identification of organisms was verified by Dr. Dan Gustafsen (aquatic species) and Dr. Mike Ivie (terrestrial adults) of Montana State University. Food habits information was summarized to Order for both number of organisms and wet weight by fish species and reach (cutthroat in allopatry or sympatric with brook trout). We weighed all whole organisms, identifiable parts, and eggs, but only counted whole organisms when summarizing by number.

Drift net samples were pooled across time periods within each site and designated as allopatric cutthroat or sympatric sites. Stomach content samples were pooled for cutthroat trout in sympatry, cutthroat trout in allopatry, and brook trout in sympatry. A food selectivity index (*L*) was computed for each species (Strauss 1979):

$$L = r_i - p_i ;$$

where, r_i represents the relative proportion of a prey item *i* in the diet and p_i is the relative proportion of a prey item *i* in the stream. The linear food index ranges between –1 (complete avoidance) and +1 (strongly selected for).

Results

Response of Westslope Cutthroat Trout to Removal of Brook Trout

Population and Biomass Estimates

It took from two to seven years to eradicate brook trout from the treatment reaches. Populations of WCT rebounded two to four years following the successful removal of brook trout (Figure 4). Estimated standing crops (g/m^2) of WCT in allopatry nearly always rebounded to levels similar to, or above, total standing crop estimates for brook trout and WCT in sympatry at the beginning of brook trout removal efforts. Interestingly, standing crops of WCT declined and rebounded twice in the upper sections of Whites Creek. First, after our initial brook trout removals and again after brook trout had re-invaded these upper sections from below (sections 3, 4, and 5, Figure 5). Total standing crops of WCT in allopatry three to four years following brook trout eradication were not significantly different then those estimated at the start of removals, when brook trout and WCT occurred in sympatry, as indicated by the overlap in standard error bars (Figure 4).

Condition Factor Effects

Spearman rank correlations were relatively low and insignificant among all variables tested, except for between condition of juvenile WCT and condition of adult WCT (positive), and condition of adult WCT and density of juvenile WCT (negative, Table 2). Best subset regression analyses for condition of juvenile WCT as the dependent variable and densities during the same year condition was measured indicated that densities of each species/size combination was included in at least one of the “good” candidate models (Table 3). All models, except the full model containing all variables, could be considered as “good”; however, the “best” model contained only estimated densities of juvenile brook trout and juvenile WCT (Table 3). When density estimates the previous year were included, the sample size was reduced from 29 to 23 and best subset analyses indicated that the five models considered as “good” all included previous year’s densities (Table 3).

Further examination of potential candidate models using least-squares linear regression analyses indicated that densities of both juvenile WCT and brook trout negatively impacted condition of juvenile WCT (Table 4). All of the other candidate models had at least one variable that did not contribute significantly ($P > 0.1$) to the model. One observation, Whites Creek during 2002, was an outlier; however, there was not a valid reason to remove this observation. Regardless, we re-ran the regression without this observation and found the estimated coefficients were similar, but the model improved, indicated by the fact that the adjusted R^2 increased from 0.131 to 0.493 and the overall model and each coefficient were more significant (Table 4).

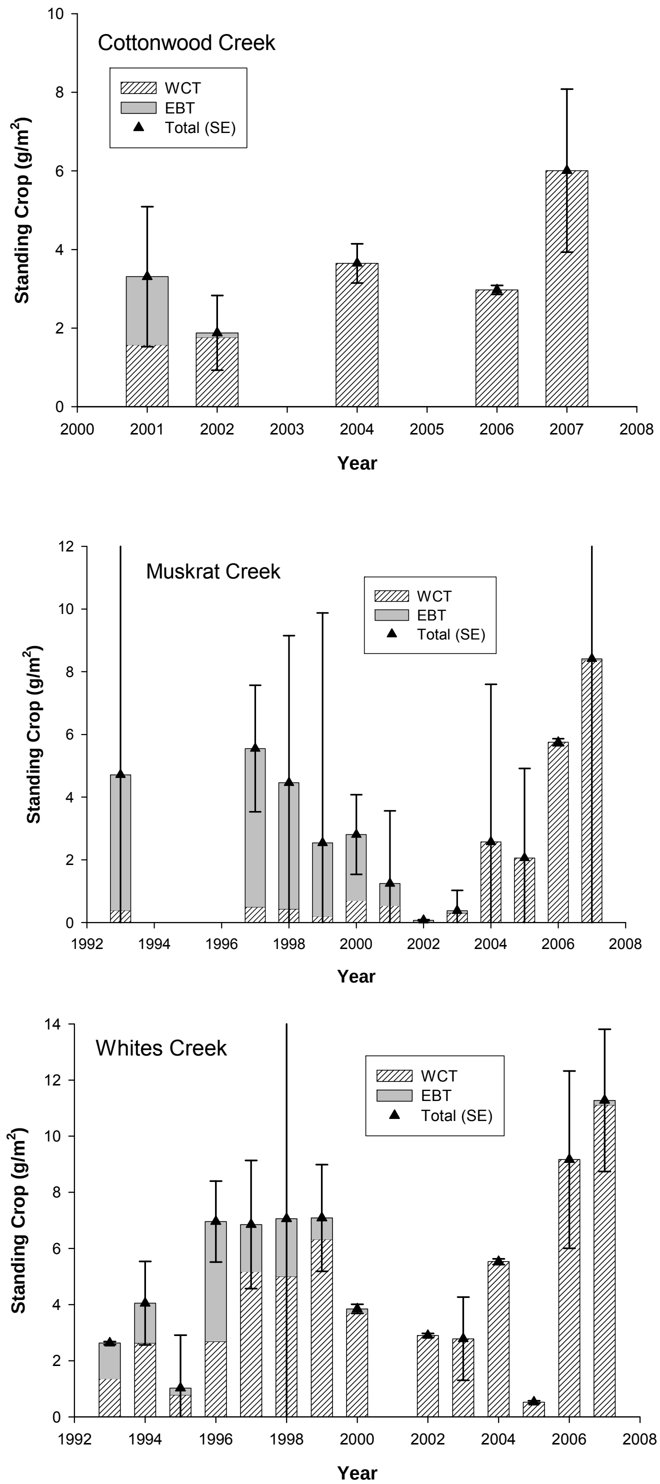


Figure 4. Standing crop estimates (g/m^2) for westslope cutthroat and brook trout 75 mm and longer by year averaged over all sample sections within treatment reaches of Cottonwood, Muskrat, and Whites creeks where brook trout were removed (EBT = brook trout; WCT = westslope cutthroat trout). Total standing crop estimate (black triangles) and associated standard errors (vertical capped lines) are shown over bars.

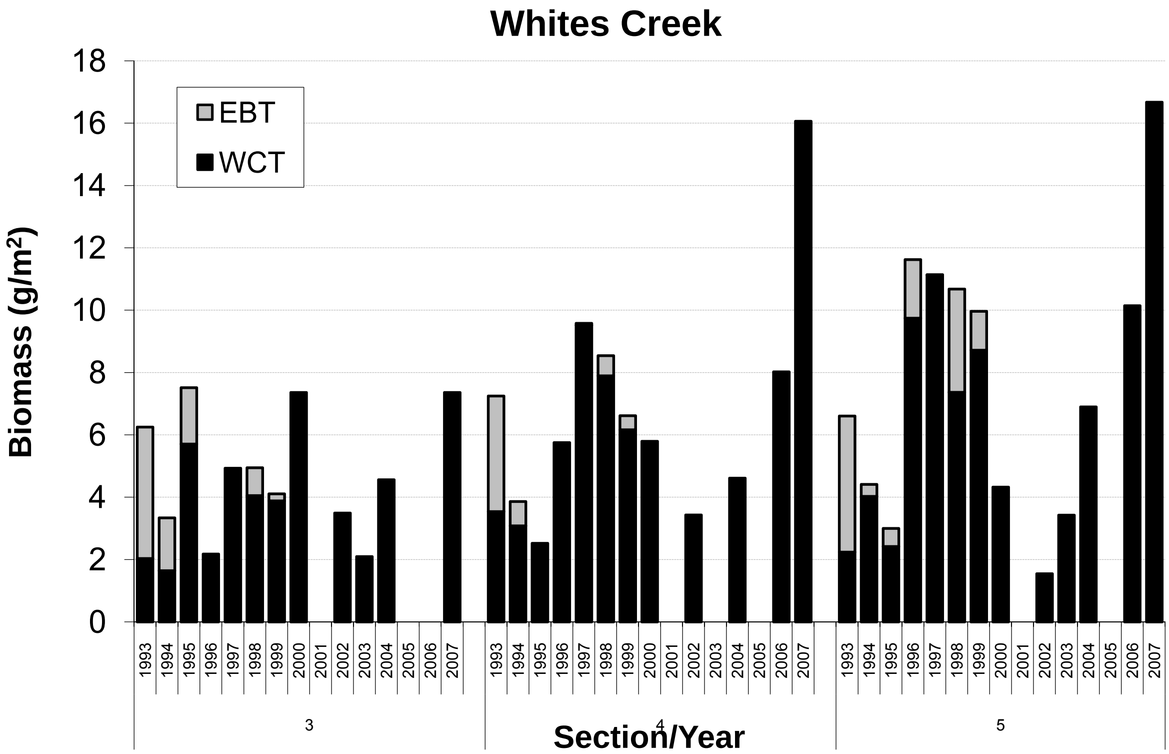


Figure 5. Standing crop estimates (g/m^2) for westslope cutthroat and brook trout 75 mm and longer by year in the upper three sample sections within the treatment reach of Whites Creek where brook trout were removed (EBT = brook trout; WCT = westslope cutthroat trout).

Table 2. Spearman rank correlation coefficients for condition of juvenile (K-juv) and adult (K-ad) cutthroat trout and densities of brook (EBT) and cutthroat (WCT) trout by size class the same year and the previous year (1yr). An asterisk indicates significance at P<0.05.

	K-juv	K-ad
K-juv	1.000	
K-ad	0.777*	1.000
EBT-juv density	-0.214	0.030
EBT-ad density	-0.148	0.130
WCT-juv density	-0.265	-0.470*
WCT-ad density	-0.229	-0.348
EBT-juv density 1yr	-0.307	-0.207
EBT-ad density 1yr	-0.361	-0.112
WCT-juv density 1yr	-0.154	-0.411
WCT-ad density 1yr	-0.207	-0.340

Table 3. Best subsets regression results for condition factor of juvenile cutthroat trout and natural log of the densities of juvenile and adult (“juv” and “ad”) brook trout (EBT) and cutthroat trout (WCT) the same year and one year previous (“prev”). “Vars” indicates number of variables in the model, R^2 is the coefficient of determination expressed as a percent, adj-R^2 is the adjusted R^2 expressed as a percent, Mallow’s *Cp* is a measure of the total mean square error with a penalty for number of independent variables, “S” is the standard error of the model. An “X” indicates the variable was included in the model. Potential candidate models are shaded in gray and the “best” models are shown in bold type.

					ln(density as #/m^2)							
Vars	R^2	adj-R^2	Mallow's C_p	S	EBT -juv	EBT -ad	WCT -juv	WCT -ad	EBT -juv prev	EBT -ad prev	WCT -juv prev	WCT -ad prev
Densities the same year (n=29)												
1	9.0	5.6	2.4	0.084524			X					
1	4.5	1.0	3.8	0.086586				X				
2	**19.3**	**13.1**	**1.3**	**0.081115**	**X**		**X**					
2	14.3	7.8	2.8	0.083562		X	X					
3	19.9	10.2	3.2	0.082429	X		X	X				
3	19.6	10.0	3.2	0.082552	X	X	X					
4	20.4	7.1	5.0	0.083840	X	X	X	X				
Densities the same and one year previous (n=23)												
2	54.9	50.4	0.4	0.046087			X		X			
3	**62.6**	**56.7**	**-0.5**	**0.043054**	**X**		**X**		**X**			
3	59.7	53.3	0.6	0.044723	X		X			X		
4	63.6	55.6	1.1	0.043623	X		X		X		X	
4	62.8	54.6	1.4	0.04411	X		X	X	X			
5	63.7	53.0	3.0	0.044842	X		X	X	X		X	
5	63.7	53.0	3.0	0.044858	X	X	X		X		X	
6	63.8	50.2	5.0	0.046169	X	X	X	X	X		X	
6	63.8	50.2	5.0	0.046197	X		X	X	X		X	X
7	63.8	46.9	7.0	0.047674	X	X	X	X	X		X	X
7	63.8	46.9	7.0	0.047683	X	X	X	X	X	X	X	
8	63.8	43.1	9.0	0.049347	X	X	X	X	X	X	X	X

Table 4. Regression analyses results evaluating the impacts of fish densities (WCT = cutthroat, EBT=brook trout, "juv" indicates juvenile density) on condition of juvenile (K-juv) and adult (K-ad) cutthroat trout. A single asterisk superscript by the variable indicates significance *P*<0.1 and a double asterisk superscript indicates significance *P*<0.05.

Dependent variable	Model	n	Adj-R^2	Model F-ratio	*P*
No Lags					
K-juv	0.788 - 0.011(ln[EBT-juv]*) - 0.033(ln[WCT-juv]**)	29	0.131	3.107	0.062
K-juv (remove outlier)	0.715 – 0.018(ln[EBT-juv]**) – 0.046(ln[WCT-juv]**)	28	0.493	14.147	<0.001
K-ad	0.917 - 0.022(ln[WCT-juv])	29	0.123	4.914	0.035
With Lags					
K-juv	0.716 - 0.011(ln[EBT-juv]*) - 0.043(ln[WCT-juv]**) - 0.009(ln[EBT-ad lagged])	23	0.567	10.606	< 0.001
K-ad	0.864 - 0.024(ln[WCT-juv]) - 0.009(ln[EBT-juv lagged])	23	0.247	4.599	0.023

When previous year's densities were included, the model that included densities of juvenile WCT the same year and both densities of brook trout the same and the prior year was the best model in terms of significance of each variable, although the prior year's densities of juvenile brook trout was marginally insignificant (P = 0.113). Both juvenile WCT densities and the previous year's juvenile brook trout densities were significantly associated with adult WCT condition.

Our analyses of the effects of year, species, and size-asymmetry on condition of individual WCT indicated that for Whites and Muskrat creeks the effect of year was marginal for all models (S.D. of year was $\leq$ 0.5 of the S.D. of the residual). In Whites Creek the simplest model that treated the effect of brook trout and WCT the same (the same coefficient and the same breadth of competition for each species) and did not include an estimate of size-asymmetry was statistically as good or better than more complex models that accounted for differences between species or included an estimate of size-asymmetry (Table 5). However, in Muskrat Creek the model that treated competition by brook trout and WCT the same, but included an estimate for size-asymmetry, was better than any other model tested (Table 5).

Effect of Brook Trout Densities on Cutthroat Trout Densities

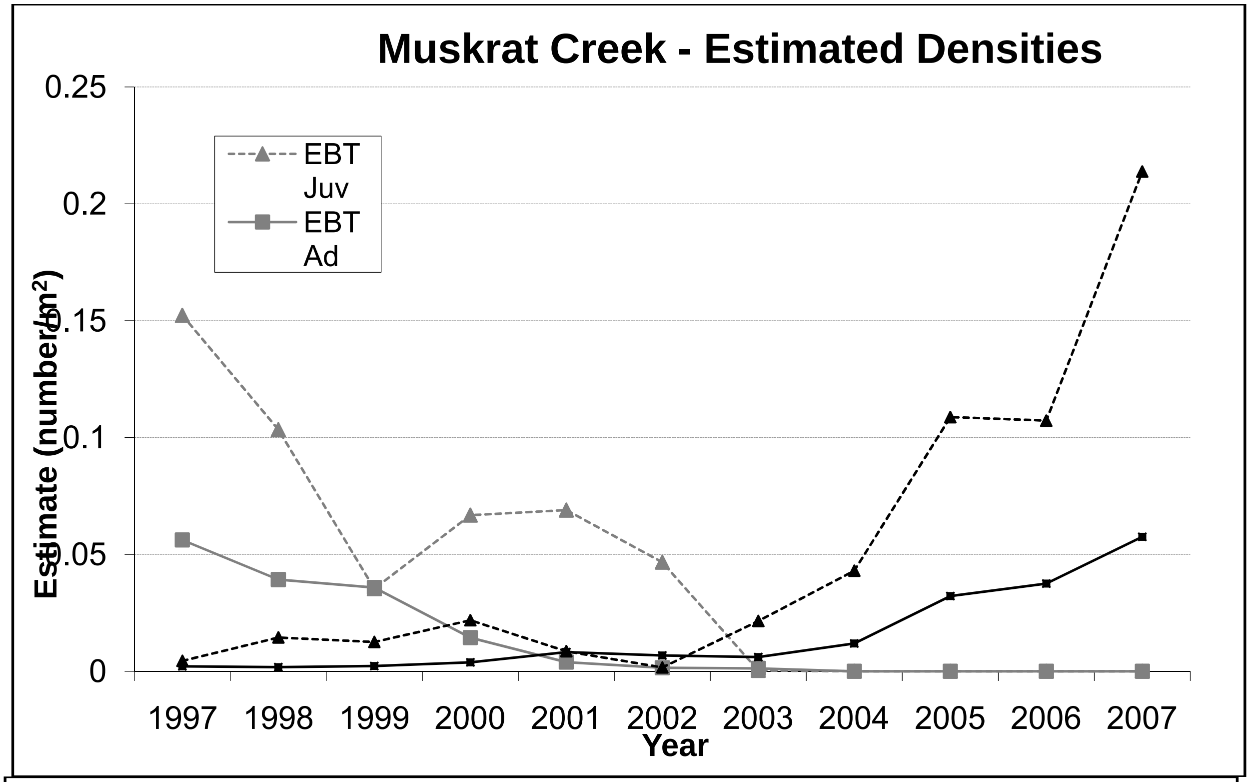
Muskrat Creek had the highest densities of brook trout at the start of removal efforts and it appeared that densities of juvenile WCT began responding to reductions in brook trout by the year 2000, but then densities of juvenile brook trout rebounded from 2000 through 2002 and both juvenile and adult WCT densities declined and remained low during this period (Figure 6; top). Then between 2002 and 2003 juvenile brook trout

Table 5. Non-linear mixed-effects model results for testing species, density, and size effects on individual condition of cutthroat trout.

Model	**a**	**b**	**WCT breadth**	**EBT breadth**	**Asymmetry**	**AIC**	**BIC**	**Δ BIC**	**LogLik**
Whites Creek only									
a=b, CT=EBT breadth, no asymmetry	**-0.0000372**	**-0.0000372**	**0.4365091**	**0.4365091**	NA	-2782.70	-2760.00	0.00	1395.35
a=b, CT=EBT breadth, = asymmetry	**-0.0000372**	**-0.0000372**	**0.4772350**	**0.4772350**	0.2352	-2782.35	-2753.97	6.03	1396.18
a<>b, CT=EBT breadth, no asymmetry	**-0.0000355**	-0.0000511	**0.4332071**	**0.4332071**	NA	-2780.82	-2752.44	7.56	1395.41
a=b, CT<>EBT breadth, no asymmetry	**-0.0000395**	**-0.0000395**	**0.4514665**	0.0075597	NA	-2779.56	-2751.18	8.82	1394.78
a<>b, CT<>EBT breadth, no asymmetry	**-0.0000364**	-0.0000484	**0.4537429**	-0.3684494	NA	-2778.99	-2744.93	15.07	1395.49
Muskrat Creek only									
a=b, CT=EBT breadth, = asymmetry	-0.0000290	-0.0000290	**-0.1823840**	**-0.1823840**	-4.4020	-1597.80	-1571.69	0.00	803.90
a=b, CT=EBT breadth, = asymmetry	-0.0000400	-0.0000400	-0.0039600	-0.0039600	124.7500	-1562.74	-1536.63	35.06	786.37
a=b, CT=EBT breadth, no asymmetry	-0.0000159	-0.0000159	-0.3774067	-0.3774067	NA	-1565.98	-1545.09	26.60	786.99
a<>b, CT=EBT breadth, no asymmetry	-0.0000077	-0.0000375	0.2854423	0.2854423	NA	-1565.16	-1539.05	32.64	787.58
a=b, CT<>EBT breadth, no asymmetry	-0.0000173	-0.0000173	0.4133052	-0.2594392	NA	-1564.16	-1538.05	33.64	787.08
a<>b, CT<>EBT breadth, no asymmetry	-0.0000100	-0.0000438	0.3887838	-0.2071536	NA	-1563.67	-1532.34	39.36	787.83

Bold values indicate significant at < 0.05

Shaded values indicate significance at < 0.10



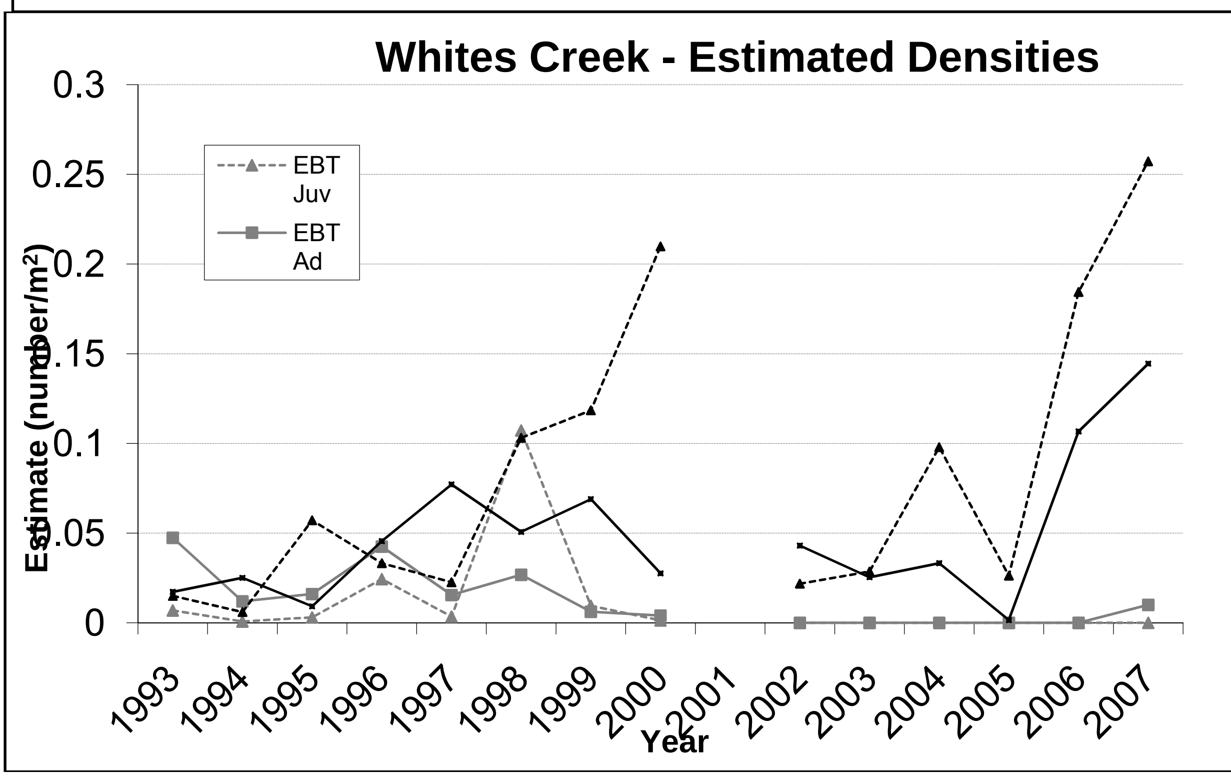


Figure 6. Estimated densities of juvenile (“Juv”) and adult (“Ad”) cutthroat (WCT) and brook trout (EBT) in reaches where brook trout were removed in Muskrat (top) and Whites (bottom) creeks.

densities declined dramatically as removal efforts became more successful and juvenile WCT densities responded by increasing dramatically from 2002 through 2007.

Whites Creek had relatively low densities of juvenile brook trout and only moderate densities of adult brook trout when removal efforts began (Figure 6; bottom), even though total standing crops of brook trout were relatively high due to the number of adult brook trout present (Figure 3; bottom graph, year 1993). Densities of juvenile WCT rose slightly in 1995, two years after brook trout removal efforts began. Then densities of juvenile WCT declined in 1997 following a rebound of both juvenile and adult brook trout densities in 1996, before climbing dramatically from 1997 through 2000 as brook trout were successfully eradicated. Densities of adult WCT lagged about one year behind densities of juveniles through 2000. After the WCT population crashed between 2000 and 2002, probably related to drought conditions and extremely high impacts to stream channel habitats from improper livestock grazing, the population rebounded dramatically through 2007.

Densities of juvenile WCT were significantly correlated to densities of both juvenile and adult brook trout and densities of adult WCT based on Spearman rank correlation coefficients (Table 6). Best subsets regression indicated that almost all variable combinations could be reasonable candidate models (Table 7); however, we tested all these models using least-squares regression and found the simplest two-variable model that did not include densities from the previous year had the highest significance for individual regression coefficients. Densities of juvenile WCT were significantly, and negatively, impacted by densities of juvenile brook trout and positively by densities of adult WCT (R^2=0.482; F-ratio=15.415; P<0.001). Adding densities from the previous year did not measurably improve model performance.

Table 6. Spearman rank correlation coefficients for densities of juvenile (WCT juv) and adult (WCT ad) cutthroat trout and densities of brook (EBT) and cutthroat (WCT) trout by size class the same year and the previous year (trailing “1”). An single asterisk indicates significance at P<0.05 and two asterisks indicate significance at P<0.001.

	WCT Juv	WCT Ad	EBT Juv	EBT Ad
WCT Juv	1.000			
WCT Ad	0.709**	1.000		
EBT Juv	-0.551*	-0.392	1.000	
EBT Ad	-0.445*	-0.247	0.873**	1.000
WCT Juv 1	0.600*	0.564*	-0.410*	-0.140
WCT Ad 1	0.432*	0.485*	-0.167	0.076
EBT Juv 1	-0.535*	-0.412*	0.790**	0.564*
EBT Ad 1	-0.469*	-0.288	0.803**	0.681**

Table 7. Best subsets regression results for natural log densities of juvenile cutthroat trout and natural log of the densities of juvenile and adult ("juv" and "ad") brook trout (EBT) and adult cutthroat trout (WCT) the same year and one year previous ("prev"). "Vars" indicates number of variables in the model, R^2 is the coefficient of determination expressed as a percent, Adj-R^2 is the adjusted R^2 expressed as a percent, Mallow's Cp is a measure of the total mean square error with a penalty for number of independent variables, "S" is the standard error of the model. An "X" indicates the variable was included in the model. Potential candidate models are shaded in gray and the "best" models are shown in bold.

					ln(density as #/m^2)					
Vars	R^2	Adj R^2	Mallow's C_p	S	EBT -juv	EBT -ad	WCT -ad	EBT -juv prev	EBT -ad prev	WCT -ad prev
Densities the same year (n=32)										
1	44.1	42.2	4.3	0.9726			X			
1	28.6	26.3	13.2	1.0987	X					
2	**51.5**	**48.2**	**2.0**	**0.9210**	**X**		**X**			
2	49.8	46.3	3.0	0.9374		X	X			
3	51.5	46.3	4.0	0.9372	X	X	X			
Densities the same and one year previous (n=26)										
2	55.0	51.0	5.0	0.8597			X	X		
3	**61.8**	**56.6**	**3.2**	**0.8095**	**X**		**X**		**X**	
4	**65.5**	**58.9**	**3.1**	**0.7879**	**X**		**X**	**X**	**X**	
4	62.7	55.7	4.7	0.8183	X	X	X		X	
5	65.7	57.2	5.0	0.8043	X	X	X	X	X	
5	65.5	56.8	5.1	0.8072	X		X	X	X	X
6	65.7	54.9	7.0	0.8252	X	X	X	X	X	X

Evaluation of Habitat Restoration

We found that there were about 440 habitat restoration projects in the Montana FWP database that had been started and completed between 1995 and 2006 (Appendix A). Of these projects 55 involved some type of stream channel restoration that included construction of pool habitats and 35 projects had instream cover additions associated with them. Our analyses of fish abundance estimates in habitat restoration treatment and nearby control sections indicated that while habitat restoration often increased densities of both cutthroat and brook trout, the proportion of brook trout was often higher within habitat restoration sections than in control sections, especially when instream cover (usually woody debris) was added as part of the restoration project (Figures 7 through 9). These findings were more obvious in streams where brook trout had become well established.

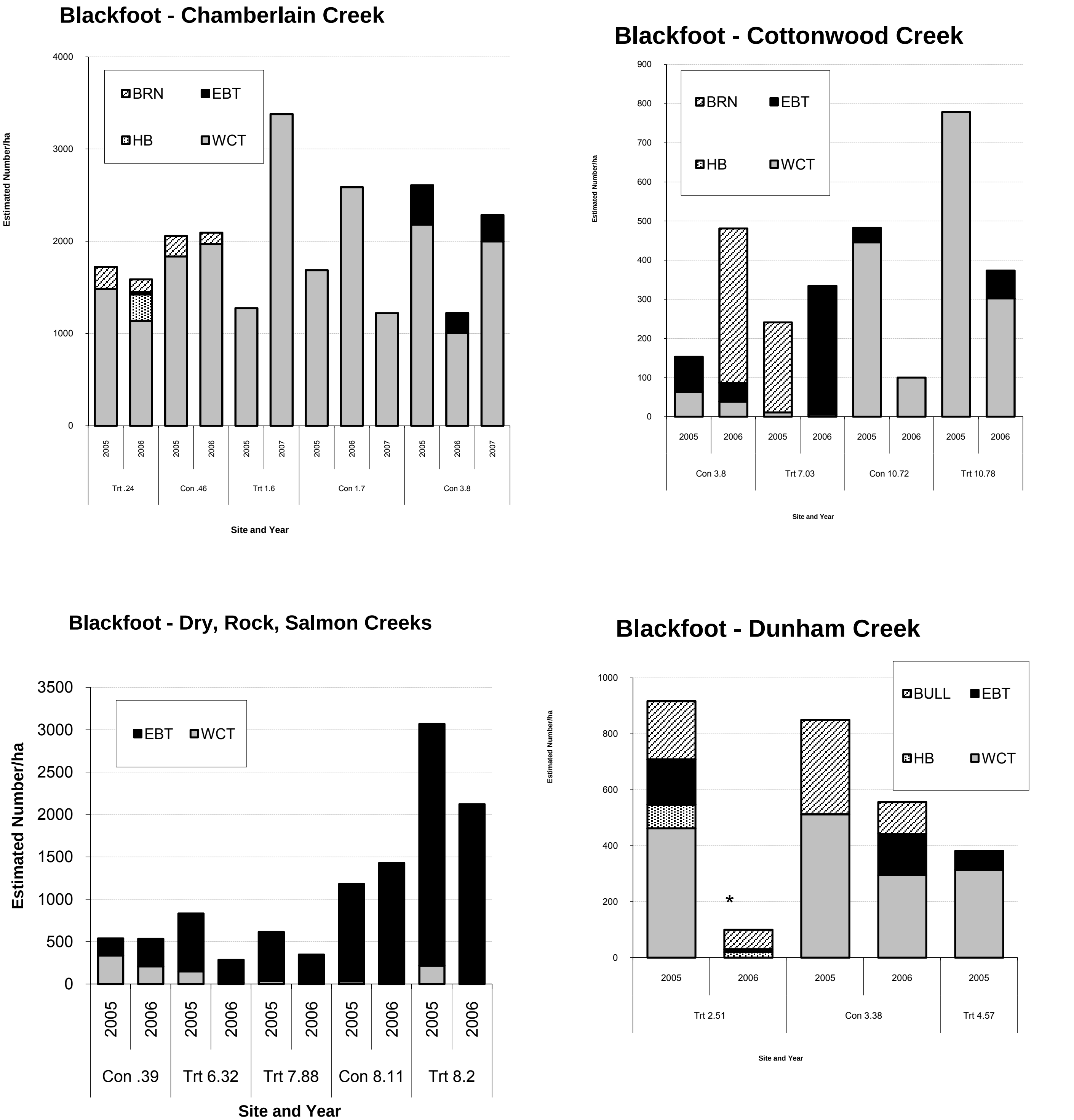


Figure 7. Estimated densities (number per ha) of fish 75 mm and longer by species (WCT = westslope cutthroat trout; HB = cutthroatXrainbow hybrids; EBT = brook trout; BRN = brown trout; and BULL = bull trout) in treatment (“Trt”) and control (“Con”) sample sections of streams in the Blackfoot River drainage of Montana. The astrick (*) above Trt 2.51 in Dunhman Creek (bottom right) indicates an estimate for WCT could not be made due to non-declining captures in 3 passes and the fact it got dark before a fourth pass could be made. All habitat projects occurred prior to 2005.

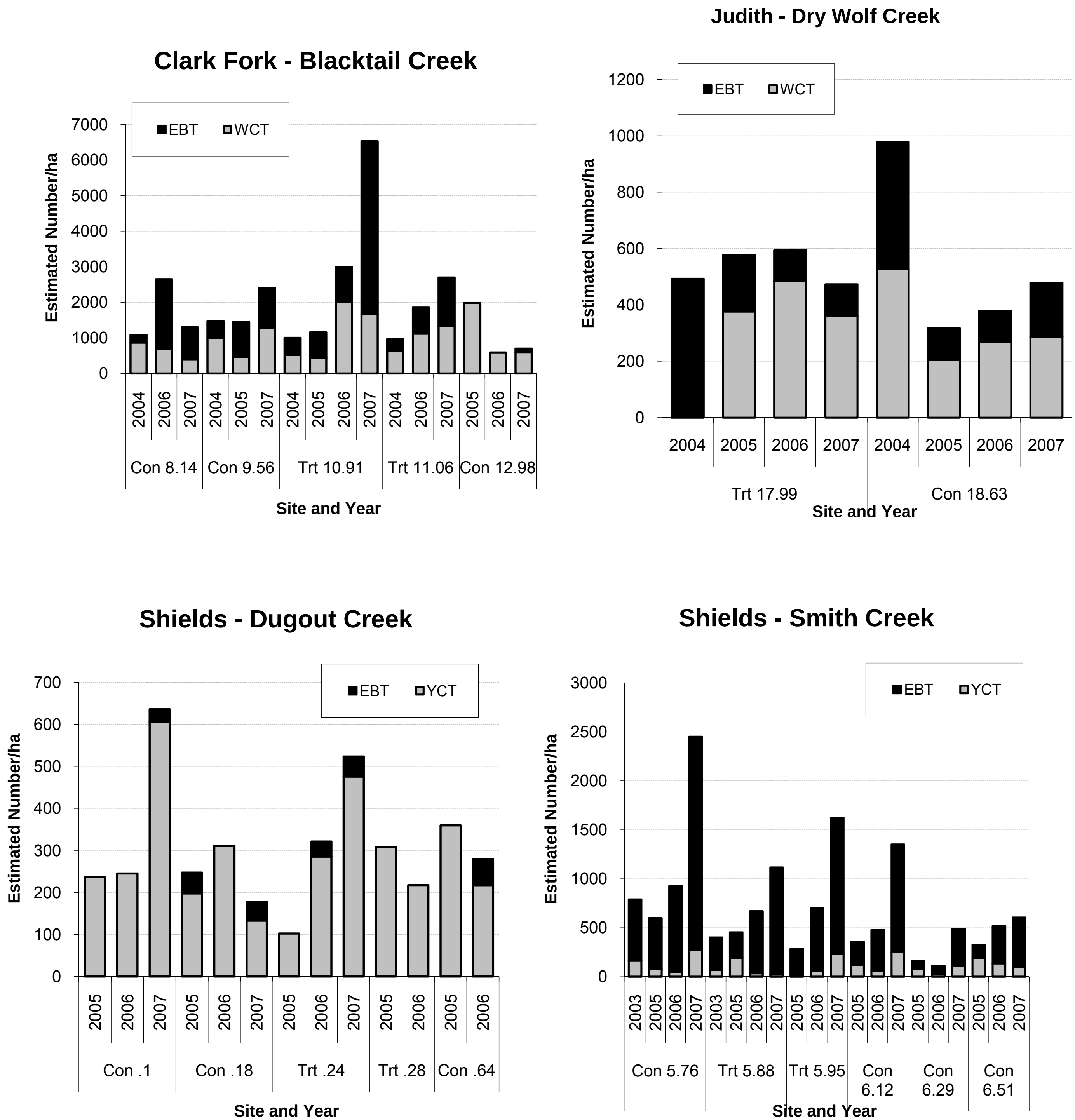


Figure 8. Estimated densities (number per ha) of fish 75 mm and longer by species (WCT = westslope cutthroat trout; EBT = brook trout) in treatment (“Trt”) and control (“Con”) sample sections of streams in the Clark Fork, Judith, and Shields River drainages of Montana. Habitat restoration projects occurred after sampling in 2005 in all the above streams, except Dry Wolf Creek where habitat restoration occurred after the 2004 sampling.

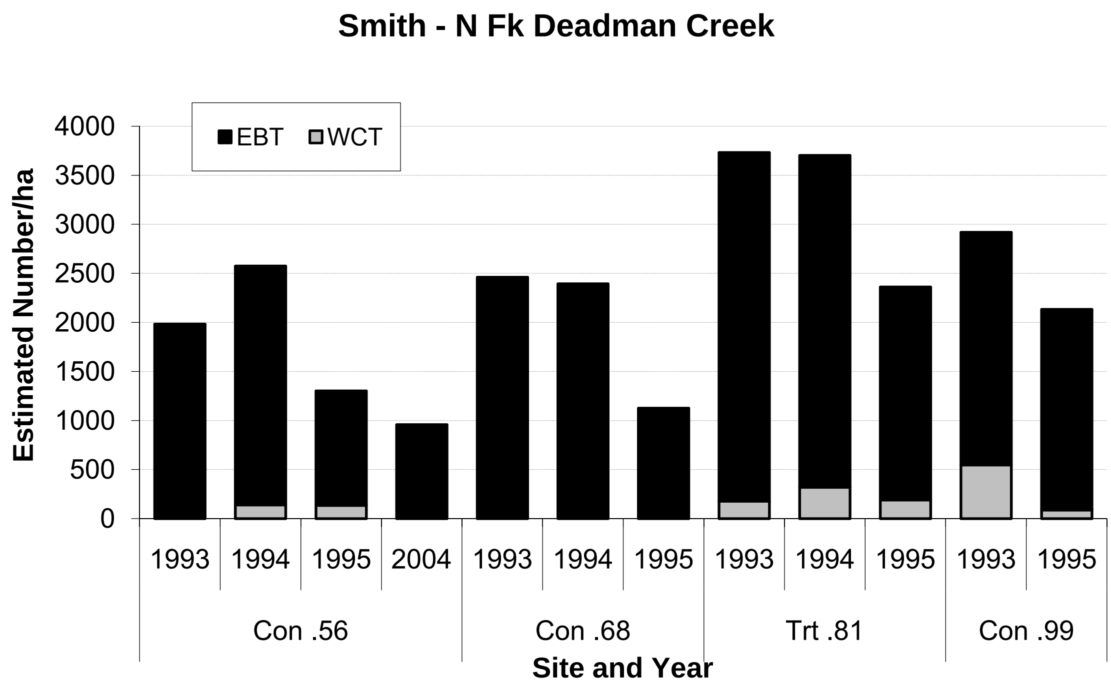


Figure 9. Estimated densities (number per ha) of fish 75 mm and longer by species (WCT = westslope cutthroat trout; HB = cutthroatXrainbow hybrids; EBT = brook trout; BRN = brown trout; and BULL = bull trout) in treatment ("Trt") and control ("Con") sample sections of streams in Smith River drainage of Montana. Note: In 2004 only brook trout were found in the lowermost section (Con .56), while no fish were found in any of the other three sections.

We were unable to rigorously evaluate the effect that additions of instream cover (woody debris) had on abundances or conditions of cutthroat trout and brook trout because during construction of those habitat restoration projects that we had designed to test these effects, our sample design protocol was not followed due to budgetary and logistics problems in the construction phase. However, during our sampling of habitat restoration projects that had instream debris installed in some pool habitats and not in others, we noticed that we captured many more brook trout from pools where instream cover was added. We observed this differential use in Dry Wolf, Smith, and Dugout creeks.

Average fish condition factors for WCT and brook trout in Blacktail Creek increased within the habitat restoration area following restoration and this increase was higher than in control sections (Figure 10). In contrast to Blacktail Creek, condition of YCT in two Shields River tributaries where habitat restoration projects were evaluated responded similarly in treatment and control sections, while brook trout condition increased in the treated sections, though not significantly (Figure 11). For those post-treatment projects we evaluated, condition factors of both cutthroat trout and brook trout were significantly higher in treated sections than in control sections. Habitat measurements in stream sections treated with habitat restoration projects and as controls for these projects documented habitat conditions within these sections over time (Tables 8 and 9).

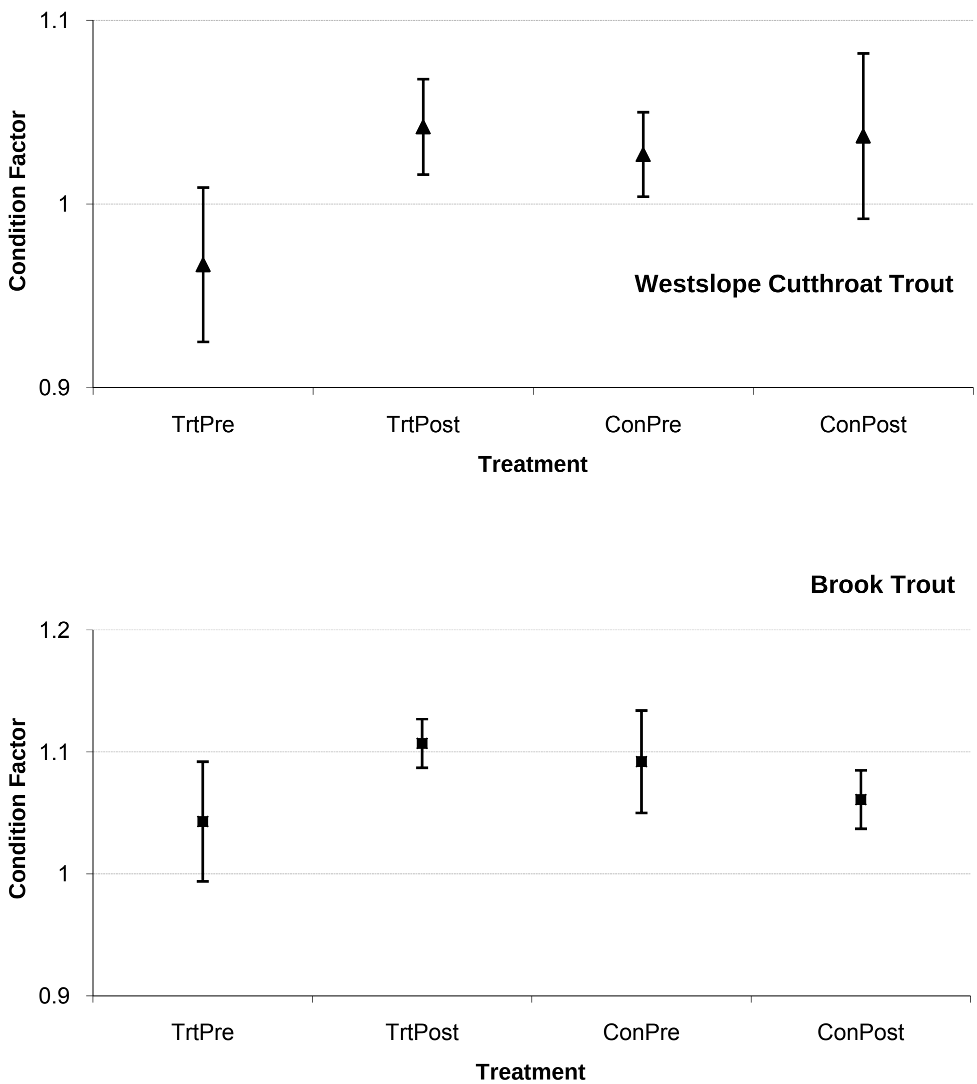
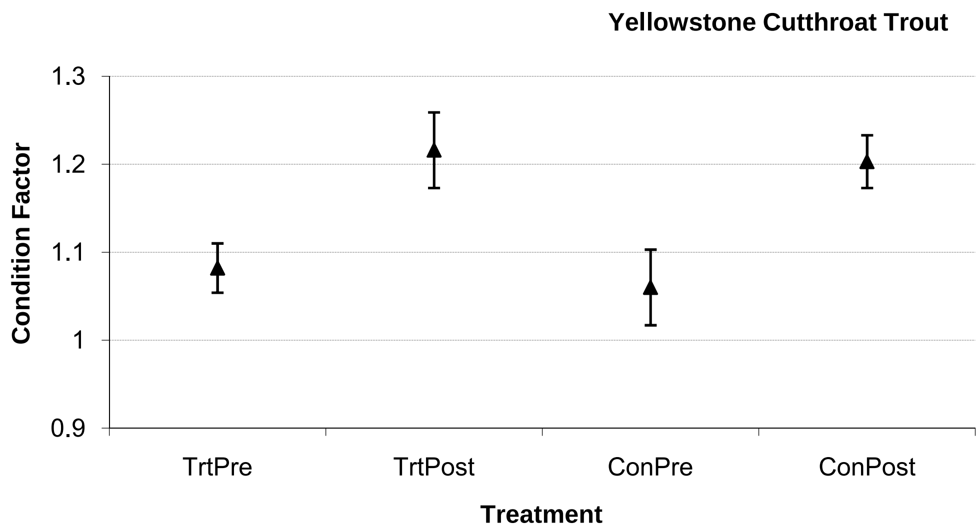


Figure 10. Average condition factors for WCT (top) and brook trout (bottom) in Blacktail Creek by treatement type (“Trt” = treated, “Con” = control) and pre- or post-treatment (“Pre” or “Post”). Vertical capped lines indicate 95% confidence intervals.



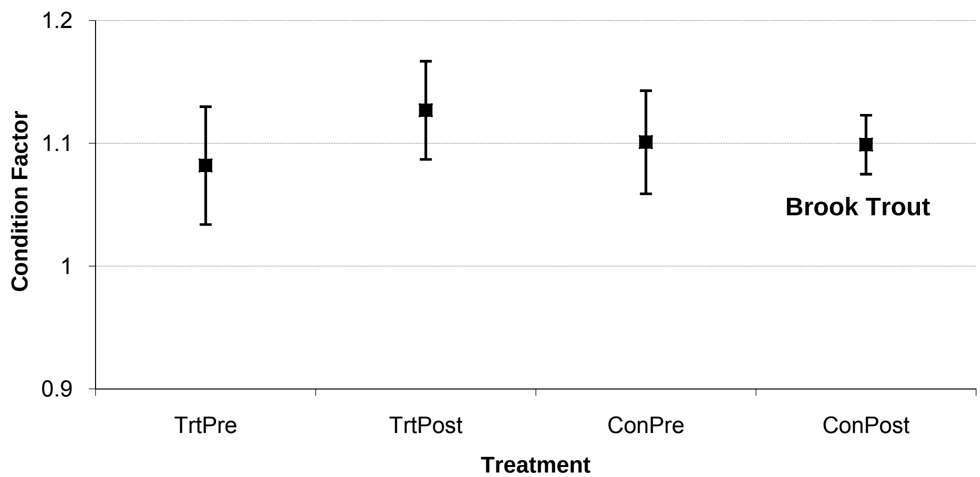


Figure 11. Average condition factors for YCT (top) and brook trout (bottom) in Dugout and Smith creeks in the Shields River drainage by treatement type ("Trt" = treated, "Con" = control) and pre- or post-treatment ("Pre" or "Post"). Vertical capped lines indicate 95% confidence intervals.

Table 8. Number (n), total length (m), average length (m), average channel and wetted widths (m), average depth (cm), and average volume (cubic meters) of each habitat type and by stream section, and average volume, thalweg depth (cm) and residual volume (cubic meters) of pools. Type of section is shown by "Habitat Enhancement codes where "Trt" is habitat enhancement treatment, "Con" is untreated control, "Pre" is before treatment occurred, and "Post" is following treatment.

RIVER STREAM **Km**	Date	Habitat Habitat type	n	Total length (m)	Average length (m)	Average width (m) Channel	 Wetted	Average depth (cm)	Volume (m^3)	Average thalweg depth (cm)	Residual pool volume (m^3)
BLACKFOOT											
CHAMBERLAIN CR											
0.4	8/17/2005		**COLLECTION**		M05067			**Habitat Enhancement Code:** TrtPost			
		POOL	8	69.0	8.6	6.0	4.1	34	12.5	50	47
		RIFFLE	11	98.0	8.9	6.5	4.1	8			
		RUN	4	33.2	8.3	5.2	3.6	15			
		For Entire Section	**23**	**200.2**	**8.7**	**6.1**	**4.0**	**18**			
0.7	8/16/2005		**COLLECTION**		M05063			**Habitat Enhancement Code:** ConPost			
		POOL	5	24.6	4.9	6.5	2.9	20	3.0	24	26
		RIFFLE	12	78.0	6.5	7.3	3.1	8			
		RUN	8	67.5	8.4	6.9	2.6	12			
		For Entire Section	**25**	**170.1**	**6.8**	**7.0**	**2.9**	**12**			
2.6	8/11/2005		**COLLECTION**		M05059			**Habitat Enhancement Code:** TrtPost			
		POOL	1	8.4	8.4	7.4	3.3	39	10.8	50	50
		RIFFLE	8	72.2	9.0	6.3	4.0	9			
		RUN	6	61.5	10.3	5.8	3.7	19			
		For Entire Section	**15**	**142.1**	**9.5**	**6.2**	**3.8**	**15**			
2.9	8/12/2005		**COLLECTION**		M05060			**Habitat Enhancement Code:** ConPost			
		POOL	3	34.5	11.5	4.8	3.3	29	9.9	45	44
		RIFFLE	8	88.4	11.1	6.1	3.6	9			
		RUN	6	50.0	8.3	6.0	3.4	19			
		For Entire Section	**17**	**172.9**	**10.2**	**5.8**	**3.4**	**16**			
6.2	8/11/2005		**COLLECTION**		M05222			**Habitat Enhancement Code:** ConPost			
		POOL	4	42.0	10.5	4.4	3.2	28	9.3	37	41
		RIFFLE	6	72.7	12.1	4.9	3.5	12			
		RUN	2	29.0	14.5	4.5	3.2	16			
		For Entire Section	**12**	**143.7**	**12.0**	**4.7**	**3.3**	**18**			
COTTONWOOD CR											
6.1	8/10/2005		**COLLECTION**		M05220			**Habitat Enhancement Code:** ConPost			
		POOL	1	14.0	14.0	10.3	5.2	43	31.3	63	48
		RIFFLE	5	103.7	20.7	9.8	7.5	16			
		RUN	3	43.0	14.3	8.3	6.6	25			
		For Entire Section	**9**	**160.7**	**17.9**	**9.4**	**6.9**	**22**			

Table 8. (continued).

Km	Date	Habitat type	n	Total length (m)	Average length (m)	Average width (m) Channel	Average width (m) Wetted	Average depth (cm)	Volume (m^3)	Average thalweg depth (cm)	Residual pool volume (m^3)
RIVER											
STREAM											
11.3	8/9/2005		**COLLECTION**	M05219				**Habitat Enhancement Code:** TrtPost			
		POOL	7	151.3	21.6	7.8	5.3	35	39.4	72	66
		RIFFLE	11	79.7	7.2	9.1	7.3	13			
		RUN	4	60.5	15.1	8.6	6.1	31			
		For Entire Section	**22**	**291.5**	**13.3**	**8.6**	**6.4**	**23**			
17.3	8/10/2005		**COLLECTION**	M05057				**Habitat Enhancement Code:** ConPost			
		POOL	1	5.0	5.0	5.8	4.7	33	7.8	47	37
		RIFFLE	5	71.0	14.2	8.1	5.5	12			
		RUN	3	32.0	10.7	6.8	4.7	17			
		For Entire Section	**9**	**108.0**	**12.0**	**7.4**	**5.1**	**16**			
17.3	8/10/2005		**COLLECTION**	M05058				**Habitat Enhancement Code:** TrtPost			
		POOL	3	30.0	10.0	7.1	3.5	26	9.3	49	37
		RIFFLE	5	59.0	11.8	10.1	5.3	12			
		RUN	2	15.0	7.5	7.1	4.8	23			
		For Entire Section	**10**	**104.0**	**10.4**	**8.6**	**4.7**	**19**			
DRY CR											
0.0	8/15/2005		**COLLECTION**	M05062				**Habitat Enhancement Code:** TrtPost			
		POOL	6	46.5	7.8	5.8	3.3	28	8.4	48	45
		RIFFLE	7	61.0	8.7	8.1	3.7	7			
		RUN	2	18.5	9.3	3.6	2.8	11			
		For Entire Section	**15**	**126.0**	**8.4**	**6.6**	**3.4**	**16**			
0.6	7/27/2005		**COLLECTION**	M05045				**Habitat Enhancement Code:** ConPost			
		POOL	3	27.9	9.3	5.3	3.8	31	11.4	45	51
		RIFFLE	10	80.4	8.0	6.2	4.1	10			
		RUN	7	52.1	7.4	6.3	3.1	20			
		For Entire Section	**20**	**160.4**	**8.0**	**6.1**	**3.7**	**17**			
DUNHAM CR											
4.0	8/12/2005		**COLLECTION**	M05061				**Habitat Enhancement Code:** TrtPost			
		POOL	2	25.5	12.8	16.4	8.6	48	53.1	63	61
		RIFFLE	6	76.0	12.7	14.6	6.1	10			
		RUN	5	90.0	18.0	20.5	7.0	21			
		For Entire Section	**13**	**191.5**	**14.7**	**17.1**	**6.8**	**20**			
4.0	7/18/2006		**COLLECTION**	M06508				**Habitat Enhancement Code:** ConPost			
		POOL	6	85.8	14.3	7.8	5.5	51	41.6	70	59
		RIFFLE	4	59.1	14.8	8.2	5.3	13			
		RUN	3	51.0	17.0	7.6	5.3	31			
		For Entire Section	**13**	**195.9**	**15.1**	**7.9**	**5.4**	**35**			
5.4	8/18/2005		**COLLECTION**	M05070				**Habitat Enhancement Code:** ConPost			
		POOL	3	44.5	14.8	13.2	6.0	38	36.4	69	61
		RIFFLE	7	49.5	7.1	17.3	6.5	13			
		RUN	3	36.0	12.0	15.4	5.5	32			
		For Entire Section	**13**	**130.0**	**10.0**	**15.9**	**6.2**	**23**			

Table 8. (continued).

RIVER STREAM Km	Date	Habitat Habitat type	n	Total length (m)	Average length (m)	Average width (m) Channel	Wetted	Average depth (cm)	Volume (m^3)	Average thalweg depth (cm)	Residual pool volume (m^3)
5.4	7/18/2006		**COLLECTION**	M06021				**Habitat Enhancement Code:** ConPost			
		POOL	3	41.9	14.0	10.2	9.0	63	84.4	69	82
		RIFFLE	2	23.2	11.6	6.4	4.5	15			
		RUN	3	62.4	20.8	6.9	4.4	26			
		For Entire Section	**8**	**127.5**	**15.9**	**8.0**	**6.1**	**37**			
7.4	8/10/2005		**COLLECTION**	M05221				**Habitat Enhancement Code:** TrtPost			
		POOL	2	35.6	17.8	14.6	3.6	19	11.3	41	49
		RIFFLE	3	42.1	14.0	13.0	4.0	5			
		RUN	1	29.2	29.2	9.2	6.5	10			
		For Entire Section	**6**	**106.9**	**17.8**	**12.9**	**4.3**	**10**			
ROCK CR											
10.2	7/29/2005		**COLLECTION**	M05050				**Habitat Enhancement Code:** TrtPost			
		POOL	4	44.5	11.1	5.3	3.8	30	12.6	43	35
		RIFFLE	5	81.5	16.3	4.6	3.3	12			
		RUN	3	23.5	7.8	4.7	3.6	23			
		For Entire Section	**12**	**149.5**	**12.5**	**4.9**	**3.5**	**21**			
12.7	7/28/2005		**COLLECTION**	M05047				**Habitat Enhancement Code:** TrtPost			
		POOL	2	22.8	11.4	4.8	4.2	27	13.6	49	45
		RIFFLE	6	73.6	12.3	5.5	4.1	15			
		RUN	4	36.2	9.1	5.9	4.5	21			
		For Entire Section	**12**	**132.6**	**11.1**	**5.5**	**4.3**	**19**			
SALMON CR											
13.1	7/29/2005		**COLLECTION**	M05048				**Habitat Enhancement Code:** ConPost			
		RIFFLE	5	57.0	11.4	2.5	2.3	15			
		RUN	5	82.5	16.5	2.5	2.3	18			
		For Entire Section	**10**	**139.5**	**14.0**	**2.5**	**2.3**	**17**			
13.2	7/28/2005		**COLLECTION**	M05046				**Habitat Enhancement Code:** TrtPost			
		POOL	3	27.6	9.2	4.3	3.0	22	6.7	35	22
		RIFFLE	4	28.1	7.0	2.8	2.1	17			
		RUN	5	65.5	13.1	2.8	2.1	17			
		For Entire Section	**12**	**121.2**	**10.1**	**3.2**	**2.3**	**18**			

Table 8. (continued).

RIVER STREAM Km	Date	Habitat type	n	Total length (m)	Average length (m)	Average width (m) Channel	Average width (m) Wetted	Average depth (cm)	Volume (m^3)	Average thalweg depth (cm)	Residual pool volume (m^3)
CLARK FORK											
BLACKTAIL CR											
13.1	6/29/2005		**COLLECTION**	M05207				**Habitat Enhancement Code:** Con			
		POOL	4	19.8	5.0	7.6	2.6	32	4.2	55	35
		RUN	5	87.0	17.4	5.6	2.1	23			
		For Entire Section	**9**	**106.8**	**11.9**	**6.5**	**2.4**	**27**			
15.4	6/28/2005		**COLLECTION**	M05206				**Habitat Enhancement Code:** Con			
		RIFFLE	2	69.5	34.8	5.6	2.8	13			
		RUN	1	3.0	3.0	4.2	1.4	22			
		For Entire Section	**3**	**72.5**	**24.2**	**5.1**	**2.3**	**16**			
17.6	6/29/2004		**COLLECTION**	M04002				**Habitat Enhancement Code:** TrtPre			
		POOL	1	5.1	5.1	3.0	2.0	30	3.1	46	37
		RIFFLE	8	62.9	7.9	3.2	2.3	16			
		RUN	10	85.2	8.5	3.3	2.6	20			
		For Entire Section	**19**	**153.2**	**8.1**	**3.3**	**2.5**	**19**			
17.6	7/11/2007		**COLLECTION**	M07522				**Habitat Enhancement Code:** TrtPost			
		POOL	4	22.7	5.7	6.2	1.9	24	2.9	41	22
		RUN	4	86.5	21.6	4.6	2.2	12			
		For Entire Section	**8**	**109.2**	**13.7**	**5.4**	**2.0**	**18**			
17.8	6/28/2004		**COLLECTION**	M04001				**Habitat Enhancement Code:** TrtPre			
		POOL	3	18.6	6.2	7.2	3.4	37	8.2	61	54
		RIFFLE	6	49.6	8.3	5.2	3.2	17			
		RUN	8	81.0	10.1	2.9	2.1	24			
		For Entire Section	**17**	**149.2**	**8.8**	**4.5**	**2.7**	**24**			
17.8	7/10/2007		**COLLECTION**	M07523				**Habitat Enhancement Code:** TrtPost			
		POOL	4	44.7	11.2	2.9	1.7	36	6.8	54	44
		RUN	6	104.0	17.3	5.0	2.2	20			
		For Entire Section	**10**	**148.7**	**14.9**	**4.1**	**2.0**	**26**			
20.9	6/27/2005		**COLLECTION**	M05203				**Habitat Enhancement Code:** Con			
		POOL	3	6.8	2.3	3.0	1.8	18	0.7	24	22
		RIFFLE	6	91.4	15.2	4.7	1.2	6			
		RUN	2	9.7	4.9	4.8	1.9	11			
		For Entire Section	**11**	**107.9**	**9.8**	**4.3**	**1.5**	**10**			

Table 8. (continued).

RIVER STREAM Km	Date	Habitat type	n	Total length (m)	Average length (m)	Average width (m) Channel	Average width (m) Wetted	Average depth (cm)	Volume (m^3)	Average thalweg depth (cm)	Residual pool volume (m^3)
JUDITH											
DRY WOLF CR											
29.0	7/18/2005		**COLLECTION**	M05215				**Habitat Enhancement Code:** TrtPost			
		POOL	8	48.8	6.1	8.4	5.8	27	9.3	60	40
		RIFFLE	7	181.5	25.9	9.5	6.0	17			
		For Entire Section	**15**	**230.3**	**15.4**	**8.9**	**5.9**	**23**			
29.0	7/18/2007		**COLLECTION**	M07526				**Habitat Enhancement Code:** TrtPost			
		POOL	9	57.2	6.4	9.4	5.7	28	11.0	49	27
		RIFFLE	9	205.2	22.8	9.9	5.9	18			
		For Entire Section	**18**	**262.4**	**14.6**	**9.6**	**5.8**	**23**			
30.0	7/20/2004		**COLLECTION**	M04017				**Habitat Enhancement Code:** ConPost			
		RIFFLE	2	160.3	80.2	11.8	5.9	16			
		RUN	3	44.5	14.8	9.3	6.0	23			
		For Entire Section	**5**	**204.8**	**41.0**	**10.3**	**6.0**	**20**			
30.0	7/20/2005		**COLLECTION**	M05218				**Habitat Enhancement Code:** ConPost			
		RIFFLE	2	177.5	88.8	8.7	6.8	16			
		RUN	1	14.7	14.7	5.7	4.0	32			
		For Entire Section	**3**	**192.2**	**64.1**	**7.7**	**5.8**	**21**			
30.0	7/18/2007		**COLLECTION**	M07525				**Habitat Enhancement Code:** ConPost			
		RIFFLE	3	181.0	60.3	10.3	6.9	15			
		RUN	1	21.0	21.0	9.5	6.1	20			
		For Entire Section	**4**	**202.0**	**50.5**	**10.1**	**6.7**	**16**			
RED ROCK											
MIDDLE FK LITTLE SHEEP CR											
20.0	8/20/1997		**COLLECTION**	M97110				**Habitat Enhancement Code:** ConPost			
		POOL	2	4.8	2.4		2.2	34	1.7	40	
		RIFFLE	8	26.4	3.3		1.4	13			
		RUN	11	49.9	4.5		1.3	25			
		For Entire Section	**21**	**81.1**	**3.9**		**1.4**	**22**			
21.1	8/20/1997		**COLLECTION**	M97109				**Habitat Enhancement Code:** ConPost			
		POOL	3	8.7	2.9		2.1	46	2.7	48	
		RIFFLE	6	32.9	5.5		2.2	10			
		RUN	8	66.9	8.4		1.9	28			
		For Entire Section	**17**	**108.5**	**6.4**		**2.0**	**25**			

Table 8. (continued).

RIVER STREAM Km	Date	Habitat type	n	Total length (m)	Average length (m)	Average width (m) Channel	Wetted	Average depth (cm)	Volume (m^3)	Average thalweg depth (cm)	Residual pool volume (m^3)
SHIELDS											
DUGOUT CR											
0.2	7/6/2005		**COLLECTION**		M05021			**Habitat Enhancement Code:** ConPre			
		POOL	2	7.1	3.6	7.7	4.8	22	3.9	26	25
		RIFFLE	4	89.4	22.4	7.0	4.1	9			
		RUN	2	10.3	5.2	4.5	2.7	28			
		For Entire Section	**8**	**106.8**	**13.4**	**6.5**	**3.9**	**17**			
0.2	6/28/2006		**COLLECTION**		M06012			**Habitat Enhancement Code:** ConPost			
		POOL	4	16.2	4.1	4.5	3.1	18	2.4	30	28
		RIFFLE	6	91.2	15.2	5.1	3.0	7			
		RUN	1	3.2	3.2	4.3	2.2	7			
		For Entire Section	**11**	**110.6**	**10.1**	**4.8**	**3.0**	**11**			
0.3	7/6/2005		**COLLECTION**		M05020			**Habitat Enhancement Code:** ConPre			
		POOL	1	3.0	3.0	4.5	2.6	28	2.2	30	30
		RIFFLE	3	86.1	28.7	6.6	4.8	12			
		RUN	2	15.6	7.8	4.4	3.1	14			
		For Entire Section	**6**	**104.7**	**17.5**	**5.5**	**3.9**	**15**			
0.3	6/28/2006		**COLLECTION**		M06011			**Habitat Enhancement Code:** ConPost			
		POOL	4	15.1	3.8	3.8	2.9	17	1.8	35	36
		RIFFLE	5	65.6	13.1	4.3	2.9	10			
		RUN	3	22.5	7.5	3.3	2.3	12			
		For Entire Section	**12**	**103.2**	**8.6**	**3.9**	**2.8**	**13**			
0.3	6/27/2007		**COLLECTION**		M07516			**Habitat Enhancement Code:** ConPost			
		POOL	2	10.7	5.4	9.3	3.3	14	2.0	21	25
		RIPPLE	2	30.5	15.3	6.7	3.5	8			
		RUN	3	26.1	8.7	6.2	3.8	8			
		For Entire Section	**7**	**67.3**	**9.6**	**7.2**	**3.5**	**9**			
0.4	6/30/2005		**COLLECTION**		M05018			**Habitat Enhancement Code:** TrtPre			
		POOL	1	4.8	4.8	9.0	5.0	15	3.6	34	32
		RIFFLE	3	84.9	28.3	9.7	4.1	10			
		RUN	2	10.3	5.2	8.6	3.1	21			
		For Entire Section	**6**	**100.0**	**16.7**	**9.2**	**3.9**	**15**			
0.4	6/28/2006		**COLLECTION**		M06013			**Habitat Enhancement Code:** TrtPost			
		POOL	1	3.8	3.8	7.8	2.5	24	2.3	30	20
		RIFFLE	6	59.2	9.9	6.8	4.4	9			
		RUN	2	7.8	3.9	6.7	2.3	14			
		For Entire Section	**9**	**70.8**	**7.9**	**6.8**	**3.7**	**11**			
0.5	7/5/2005		**COLLECTION**		M05019			**Habitat Enhancement Code:** TrtPre			
		POOL	2	4.7	2.4	3.6	2.3	27	1.3	34	36
		RIFFLE	4	93.5	23.4	10.3	4.6	8			
		RUN	2	5.6	2.8	6.7	3.6	16			
		For Entire Section	**8**	**103.8**	**13.0**	**7.7**	**3.7**	**15**			

Table 8. (continued).

RIVER STREAM Km	Date	Habitat type	n	Total length (m)	Average length (m)	Average width (m) Channel	Average width (m) Wetted	Average depth (cm)	Volume (m^3)	Average thalweg depth (cm)	Residual pool volume (m^3)
0.5	6/28/2006		**COLLECTION**	M06502				**Habitat Enhancement Code:** TrtPost			
		POOL	5	16.0	3.2	4.7	3.2	17	1.9	25	21
		RIFFLE	8	79.1	9.9	7.4	3.4	8			
		RUN	4	29.3	7.3	7.1	2.9	12			
		For Entire Section	**17**	**124.4**	**7.3**	**6.6**	**3.2**	**11**			
1.0	7/11/2005		**COLLECTION**	M05027				**Habitat Enhancement Code:** ConPre			
		POOL	2	8.8	4.4	4.1	1.9	21	1.5	34	24
		RIFFLE	4	65.0	16.3	4.1	2.3	9			
		RUN	3	27.3	9.1	3.8	2.3	20			
		For Entire Section	**9**	**101.1**	**11.2**	**4.0**	**2.2**	**15**			
1.0	6/28/2006		**COLLECTION**	M06501				**Habitat Enhancement Code:** ConPost			
		POOL	2	12.8	6.4	3.5	2.3	25	3.7		
		RIFFLE	4	54.7	13.7	4.2	2.8	9			
		RUN	2	22.9	11.5	5.4	2.5	20			
		For Entire Section	**8**	**90.4**	**11.3**	**4.3**	**2.6**	**15**			
SMITH CR											
9.3	7/11/2005		**COLLECTION**	M05028				**Habitat Enhancement Code:** ConPre			
		RIFFLE	5	66.2	13.2	6.7	4.1	10			
		RUN	4	47.0	11.8	5.2	3.4	17			
		For Entire Section	**9**	**113.2**	**12.6**	**6.1**	**3.8**	**13**			
9.3	6/27/2006		**COLLECTION**	M06010				**Habitat Enhancement Code:** ConPost			
		POOL	5	38.0	7.6	4.2	3.3	16	3.9	29	23
		RIFFLE	5	68.1	13.6	5.8	4.6	8			
		RUN	1	9.2	9.2	4.1	3.0	11			
		For Entire Section	**11**	**115.3**	**10.5**	**4.9**	**3.8**	**12**			
9.5	6/27/2006		**COLLECTION**	M06009				**Habitat Enhancement Code:** TrtPost			
		POOL	3	11.2	3.7	4.3	3.6	17	2.2	32	25
		RIFFLE	9	66.8	7.4	3.9	2.9	10			
		RUN	5	30.0	6.0	3.1	2.5	15			
		For Entire Section	**17**	**108.0**	**6.4**	**3.8**	**2.9**	**13**			
9.5	6/25/2007		**COLLECTION**	M07001				**Habitat Enhancement Code:** TrtPost			
		RIFFLE	6	65.4	10.9	4.4	3.2	10			
		RUN	4	29.7	7.4	5.0	3.1	13			
		For Entire Section	**10**	**95.1**	**9.5**	**4.7**	**3.2**	**11**			
9.6	7/7/2005		**COLLECTION**	M05023				**Habitat Enhancement Code:** TrtPre			
		POOL	1	6.8	6.8	6.4	2.7	21	3.9	30	27
		RIFFLE	5	83.3	16.7	6.1	3.3	11			
		RUN	4	26.0	6.5	5.4	2.9	16			
		For Entire Section	**10**	**116.1**	**11.6**	**5.8**	**3.1**	**14**			

Table 8. (continued).

RIVER

STREAM Km	Date	Habitat Habitat type	n	Total length (m)	Average length (m)	Average width (m) Channel	Wetted	Average depth (cm)	Volume (m^3)	Average thalweg depth (cm)	Residual pool volume (m^3)
9.6	6/27/2006		**COLLECTION**		M06008			**Habitat Enhancement Code:** TrtPost			
		POOL	2	10.8	5.4	4.4	3.1	23	3.8	34	33
		RIFFLE	7	73.1	10.4	6.2	3.0	12			
		RUN	5	31.3	6.3	6.6	3.3	15			
		For Entire Section	**14**	**115.2**	**8.2**	**6.1**	**3.1**	**15**			
9.6	6/26/2007		**COLLECTION**		M07512			**Habitat Enhancement Code:** TrtPost			
		POOL	1	3.5	3.5	16.6	4.0	12	1.7	31	18
		RIFFLE	3	87.0	29.0	12.3	3.3	12			
		RUN	3	25.6	8.5	10.2	3.5	14			
		For Entire Section	**7**	**116.1**	**16.6**	**12.0**	**3.5**	**13**			
9.7	6/27/2007		**COLLECTION**		M07004			**Habitat Enhancement Code:** ConPost			
		POOL	2	11.3	5.7	7.2	3.0	18	2.8	18	23
		RIFFLE	5	90.7	18.1	6.2	2.8	8			
		RUN	2	23.6	11.8	7.2	2.9	13			
		For Entire Section	**9**	**125.6**	**14.0**	**6.6**	**2.8**	**11**			
9.8	7/8/2005		**COLLECTION**		M05024			**Habitat Enhancement Code:** ConPre			
		POOL	1	7.0	7.0	9.2	3.4	23	5.5	44	33
		RIFFLE	4	54.3	13.6	8.8	5.1	12			
		RUN	3	34.8	11.6	5.6	3.3	16			
		For Entire Section	**8**	**96.1**	**12.0**	**7.6**	**4.2**	**15**			
9.8	6/26/2006		**COLLECTION**		M06005			**Habitat Enhancement Code:** ConPost			
		POOL	2	14.8	7.4	3.2	3.0	18	3.6	42	34
		RIFFLE	6	56.4	9.4	5.0	4.2	10			
		RUN	4	33.3	8.3	3.7	2.9	13			
		For Entire Section	**12**	**104.5**	**8.7**	**4.3**	**3.6**	**12**			
9.8	6/26/2007		**COLLECTION**		M07513			**Habitat Enhancement Code:** ConPost			
		POOL	2	16.0	8.0	13.5	5.5	24	9.9	24	25
		RIFFLE	6	112.0	18.7	12.3	6.4	10			
		RUN	4	36.6	9.2	11.8	5.0	14			
		For Entire Section	**12**	**164.6**	**13.7**	**12.3**	**5.8**	**14**			
10.1	7/8/2005		**COLLECTION**		M05025			**Habitat Enhancement Code:** ConPost			
		POOL	1	3.0	3.0	5.7	3.8	17	1.9	27	16
		RIFFLE	6	63.1	10.5	7.7	3.5	11			
		RUN	5	41.4	8.3	7.9	3.2	11			
		For Entire Section	**12**	**107.5**	**9.0**	**7.6**	**3.4**	**11**			
10.1	6/26/2006		**COLLECTION**		M06006			**Habitat Enhancement Code:** ConPost			
		POOL	2	11.9	6.0	5.2	4.3	15	3.6	33	17
		RIFFLE	7	65.6	9.4	4.4	3.5	10			
		RUN	5	36.9	7.4	3.6	2.8	13			
		For Entire Section	**14**	**114.4**	**8.2**	**4.2**	**3.4**	**12**			

Table 8. (continued).

RIVER

STREAM Km	Date	Habitat type	n	Total length (m)	Average length (m)	Average width (m) Channel	Average width (m) Wetted	Average depth (cm)	Volume (m^3)	Average thalweg depth (cm)	Residual pool volume (m^3)
10.5	7/8/2005		**COLLECTION**	M05026				**Habitat Enhancement Code:** ConPost			
		POOL	4	29.8	7.5	5.5	3.5	25	6.3	40	39
		RIFFLE	6	32.9	5.5	5.6	3.9	13			
		RUN	5	38.6	7.7	5.4	3.6	15			
		For Entire Section	**15**	**101.3**	**6.8**	**5.5**	**3.7**	**17**			
10.5	6/26/2006		**COLLECTION**	M06007				**Habitat Enhancement Code:** ConPost			
		POOL	6	37.8	6.3	3.8	3.2	20	4.0	41	31
		RIFFLE	7	39.9	5.7	4.8	4.2	10			
		RUN	4	27.6	6.9	4.2	3.5	14			
		For Entire Section	**17**	**105.3**	**6.2**	**4.3**	**3.7**	**14**			
SMITH											
N FK DEADMAN CR											
0.9	8/16/1993		**COLLECTION**	M93130				**Habitat Enhancement Code:** ConPost			
		POOL	3	13.4	4.5		2.6	17	2.4	37	
		RIFFLE	5	76.2	15.2		2.2				
		For Entire Section	**8**	**89.6**	**11.2**		**2.4**	**17**			
1.1	8/16/1993		**COLLECTION**	M93129				**Habitat Enhancement Code:** ConPost			
		POOL	2	4.5	2.3		2.6	16	1.0	29	
		RIFFLE	6	44.1	7.4		1.9				
		RUN	5	21.7	4.3		1.9				
		For Entire Section	**13**	**70.3**	**5.4**		**2.0**	**16**			
1.3	8/16/1993		**COLLECTION**	M93131				**Habitat Enhancement Code:** TrtPost			
		POOL	6	23.5	3.9		2.3	16	1.6	39	
		RIFFLE	6	53.9	9.0		1.8				
		RUN	2	9.8	4.9		1.5				
		For Entire Section	**14**	**87.2**	**6.2**		**1.9**	**16**			
1.3	7/21/2004		**COLLECTION**	M04019				**Habitat Enhancement Code:** TrtPost			
		POOL	3	9.2	3.1	5.3	1.8	11	0.6	23	21
		RIFFLE	4	93.3	23.3	4.5	1.2	5			
		For Entire Section	**7**	**102.5**	**14.6**	**4.8**	**1.5**	**8**			
1.6	8/17/1993		**COLLECTION**	M93125				**Habitat Enhancement Code:** ConPost			
		POOL	7	18.5	2.6		1.2	18	0.6	38	
		RIFFLE	10	38.1	3.8		1.5				
		RUN	4	19.1	4.8		1.6				
		For Entire Section	**21**	**75.7**	**3.6**		**1.4**	**18**			

Table 9. Streambed composition, frequency of small (< 150 mm) and large (>= 150 mm) in-channel and cross-channel woody debris per km, and square meters of spawning habitat per km by stream, section, and date.

RIVER STREAM Section Km	Date	Streambed composition (% by class)						Frequency (# km) of woody debris by size				Square meters of spawning habitat per km
								In-channel		Cross-channel		
		Boulder	Cobble	Lg Grav	Sm Grav	Sand	Silt	Small	Large	Small	Large	
BLACKFOOT												
CHAMBERLAIN CR												
0.4	8/17/2005	10	30	30	15	5	10	540	210	0	20	340.0
0.7	8/16/2005	15	20	20	20	10	15	959	171	35	29	252.9
2.6	8/11/2005	5	20	35	20	5	15	1152	359	0	14	24.1
2.9	8/12/2005	20	30	20	10	5	15	715	180	12	23	52.3
6.2	8/11/2005	10	35	25	10	8	12	1171	157	0	14	89.3
COTTONWOOD CR												
6.1	8/10/2005	10	30	20	15	10	15	1238	63	0	0	65.6
11.3	8/9/2005	0	10	40	30	10	10	569	14	0	3	441.4
17.3	8/10/2005	15	35	30	10	5	5	971	57	0	0	81.0
17.3	8/10/2005	10	40	30	10	5	5	610	76	0	0	104.8
DRY CR												
0.5	8/15/2005	0	5	45	25	20	5	369	38	0	8	907.7
0.6	7/27/2005	2	13	45	25	10	5	675	200	0	6	2590.6
DUNHAM CR												
4.0	8/12/2005	5	30	35	20	5	5	1447	205	0	32	821.1
4.0	7/18/2006	5	25	35	25	10	5	750	344	0	31	303.1
5.4	8/18/2005	5	40	25	10	10	10	754	331	0	0	476.9
5.4	7/18/2006	5	25	35	20	15	10	2800	800	0	120	600.0
7.4	8/10/2005	10	40	30	10	5	5	124	86	0	29	42.9
ROCK CR												
10.2	7/29/2005	5	25	25	20	10	15	47	113	0	33	273.3
12.7	7/28/2005	3	12	30	40	15	10	1200	246	0	0	861.5

Table 9. (continued).

RIVER STREAM		Streambed composition (% by class)						Frequency (# km) of woody debris by size				Square meters of spawning habitat per km
								In-channel		Cross-channel		
Section Km	Date	Boulder	Cobble	Lg Grav	Sm Grav	Sand	Silt	Small	Large	Small	Large	
SALMON CR												
13.1	7/29/2005	0	10	30	30	15	15	36	0	0	0	342.9
13.2	7/28/2005	0	10	20	45	15	10	33	83	0	0	316.7
CLARK FORK												
BLACKTAIL CR												
13.1	6/29/2005	0	0	15	50	35	0	1860	50	120	0	132.5
15.4	6/28/2005	30	20	30	10	10	0	480	107	0	53	16.7
17.6	6/29/2004	20	0	5	10	55	10	573	33	40	13	7.3
17.6	7/11/2007	5	2		45	22	26	1500	270	450	200	30.0
17.8	6/28/2004	5	0	0	5	80	10	587	7	47	0	5.3
17.8	7/10/2007	5	1	10	35	21	28	547	13	147	0	6.7
20.9	6/27/2005	10	15	30	10	25	10	650	120	40	30	5.0
JUDITH												
DRY WOLF CR												
29.0	7/18/2005	15	70	15	0	0	0	65	43	0	13	0.0
29.0	7/18/2007	75	20	2	2	1	0	87	27	0	13	1.7
30.0	7/20/2004	20	60	10	5	3	2	54	15	0	0	2.5
30.0	7/20/2005	10	60	25	5	0	0	135	30	0	30	12.5
30.0	7/18/2007	70	18	5	5	2		243	30	0	13	0.0
RED ROCK												
MIDDLE FK LITTLE SHEEP CR												
20.0	8/20/1997	2	5	10	10	13	60	170	0	0	0	0.0
21.1	8/20/1997	1	14	12	13	10	50	890	0	40	0	0.0

Table 9. (continued).

RIVER STREAM Section Km	Date	Streambed composition (% by class) Boulder	Cobble	Lg Grav	Sm Grav	Sand	Silt	Frequency (# km) of woody debris by size In-channel Small	In-channel Large	Cross-channel Small	Cross-channel Large	Square meters of spawning habitat per km
SHIELDS												
DUGOUT CR												
0.2	7/6/2005	5	25	35	20	5	10	785	75	0	75	9.3
0.2	6/28/2006	10	40	20	10	15	5	445	127	0	73	118.2
0.3	7/6/2005	10	25	25	20	5	15	400	48	0	0	2.9
0.3	6/28/2006	20	55	10	5	5	5	638	200	0	57	19.0
0.3	6/27/2007	45	40	5		10		1160	147	93	40	10.0
0.4	6/30/2005	10	50	20	5	5	10	440	120	10	50	15.0
0.4	6/28/2006	10	40	25	15	13	2	1187	307	0	120	130.0
0.5	7/5/2005	5	45	25	10	5	10	615	87	29	58	2.4
0.5	6/28/2006	5	30	25	25	15	0	440	608	16	136	172.0
1.0	7/11/2005	5	30	35	10	15	5	490	110	0	40	2.5
1.0	6/28/2006	10	45	20	15	5	5	496	120	0	40	96.0
SMITH CR												
9.3	7/11/2005	5	20	35	20	10	10	173	55	9	9	18.2
9.3	6/27/2006	5	30	25	20	15	5	645	136	0	9	272.7
9.5	7/7/2005	5	35	20	15	15	10	369	146	0	10	24.3
9.5	6/27/2006	15	55	15	10	10	5	670	214	0	49	72.8
9.5	6/25/2007	30	60	5		5		238	248	86	57	50.5
9.6	7/7/2005	15	40	15	10	10	10	122	17	0	0	34.8
9.6	6/27/2006	15	55	15	12	10	8	200	165	0	78	47.8
9.6	6/26/2007	50	40	7		3		417	122	0	70	20.0
9.7	6/27/2007	40	40	10		10		840	296	40	96	28.0
9.8	7/8/2005	10	40	15	10	10	15	290	10	0	10	16.0
9.8	6/26/2006	17	35	10	10	20	8	350	120	0	50	30.0
9.8	6/26/2007	40	50	5		5		460	100	10	40	13.0
10.1	7/8/2005	15	35	20	10	10	10	157	37	0	0	27.8
10.1	6/26/2006	15	40	13	12	15	5	130	74	0	0	60.2
10.5	7/8/2005	15	40	20	10	10	15	620	190	0	100	90.0
10.5	6/26/2006	25	35	10	10	10	10	730	250	10	90	260.0

Table 9. (continued).

RIVER STREAM Section Km	Date	Streambed composition (% by class) Boulder	Cobble	Lg Grav	Sm Grav	Sand	Silt	Frequency (# km) of woody debris by size In-channel Small	In-channel Large	Cross-channel Small	Cross-channel Large	Square meters of spawning habitat per km
SMITH												
N FK DEADMAN CR												
0.9	8/16/1993	15	40	20	10	10	5	78	324	0	0	25.7
1.1	8/16/1993	10	45	25	15	10	5	199	228	0	0	24.2
1.3	8/16/1993	10	20	30	20	15	5	161	241	0	0	22.9
1.3	7/21/2004	50	30	10	5	5	5	180	80	50	60	2.5
1.6	8/17/1993	15	45	15	10	10	5	145	489	0	26	55.5

Comparative Food Habitats

In both Whites and Muskrat creeks there was a noticeable hatch of adult terrestrial Lepidopterans (budworm moths of the Family Tortricidae; Figures 10 through 12 and 14 through 16) and in Muskrat Creek these moths dominated both the drift and stomach contents making it difficult to discern any differences in food habits, especially when proportions were based on weights of organisms (Figure 12). However, in Muskrat Creek when proportions of food items were based on number of items, we observed a slightly higher proportion of Ephemeropterans consumed by allopatric westslope cutthroat trout, then either westslope cutthroat trout or brook trout in sympatry (Figure 13). Cutthroat in allopatry were eating a higher proportion of Ephemeropterans than those in sympatry despite the fact that more Ephemeropterans were found in the drift in the sympatric site (Figure 14). The lack of observed differences when proportions were based on weights was due partly because budworm moths weighed more than Ephemeropterans (Figure 12). Adult budworm moths (Lepidopterans) were selected by all groups (Figure 15).

By contrast, in Whites Creek, where the adult budworm moth hatch was much less abundant than in Muskrat Creek, we observed that allopatric westslope cutthroat trout consumed a higher proportion of Ephemeropterans (computed by number or by weight) than either cutthroat trout or brook trout in sympatry (Figures 16 and 17). While there were more “Other” organisms (including unidentified organisms) in stomachs of cutthroat trout collected in sympatry with brook trout, the combination of proportions of “Other” organisms and Ephemeropterans from these stomachs still did not equal the proportion of Ephemeropterans in stomachs of cutthroat trout in allopatry. The proportion of Ephemeropterans available in the drift did not explain the high use of this Order by cutthroat trout in allopatry (Figure 18).

Cutthroat trout in Whites Creek were selecting for Ephemeropterans and against Lepidopterans in allopatry, but were selecting against Ephemeropterans and for Lepidopterans in sympatry with brook trout (Figure 19). This switch might be explained by cutthroat trout competing against brook trout for benthic positions to feed on aquatic macroinvertebrate drift or benthic organisms, but being able to feed on adult terrestrial Lepidopterans on the water’s surface with less competitive interference. Both species, especially the smaller individuals, appeared to select for Dipterans.

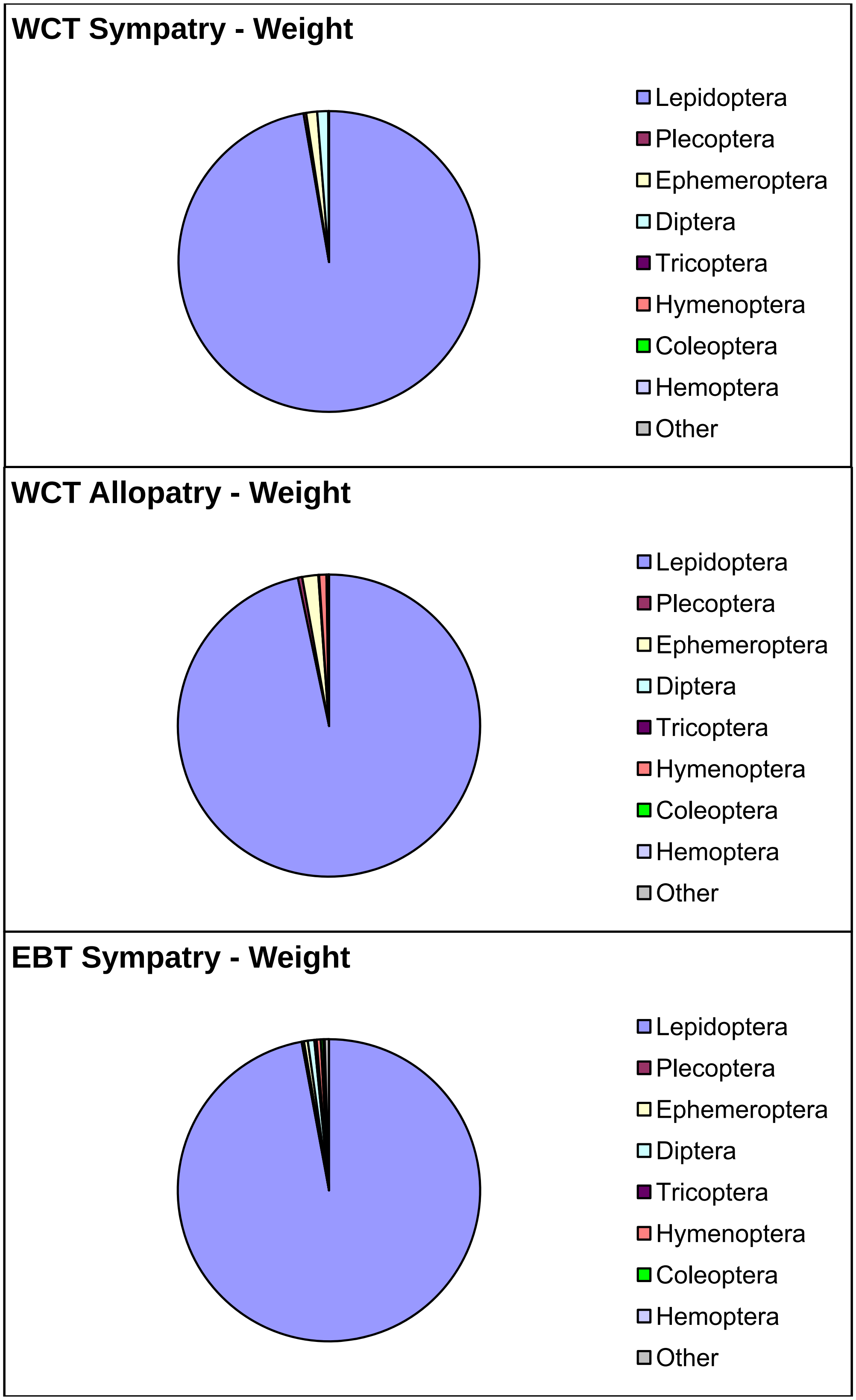
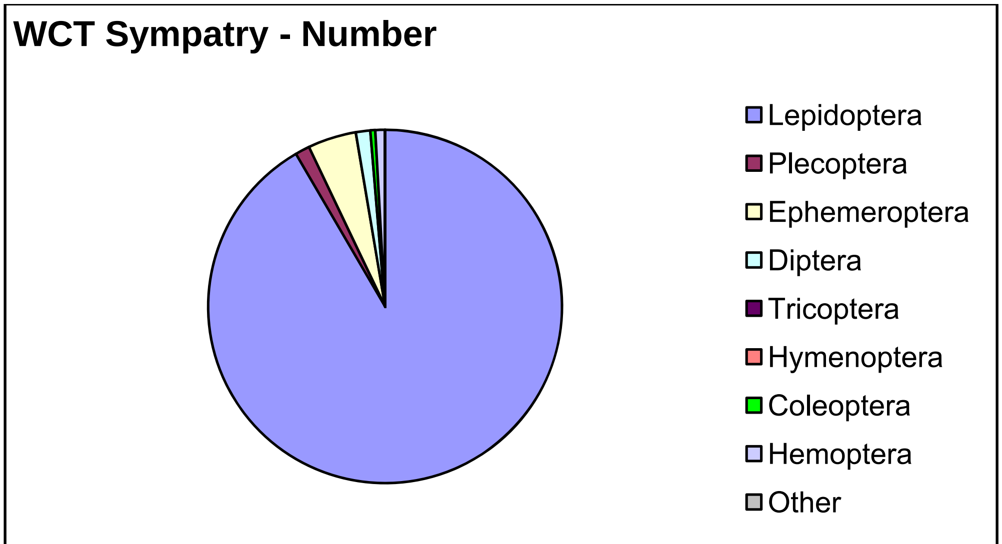
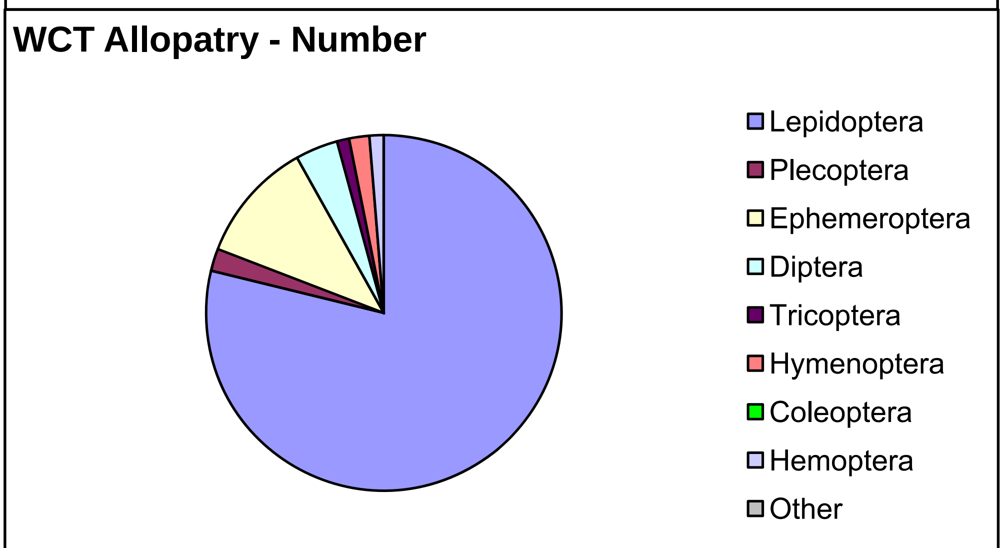


Figure 12. Proportion of the weight of food items by Order in westslope cutthroat trout (WCT) and brook trout (EBT) stomachs in Muskrat Creek.





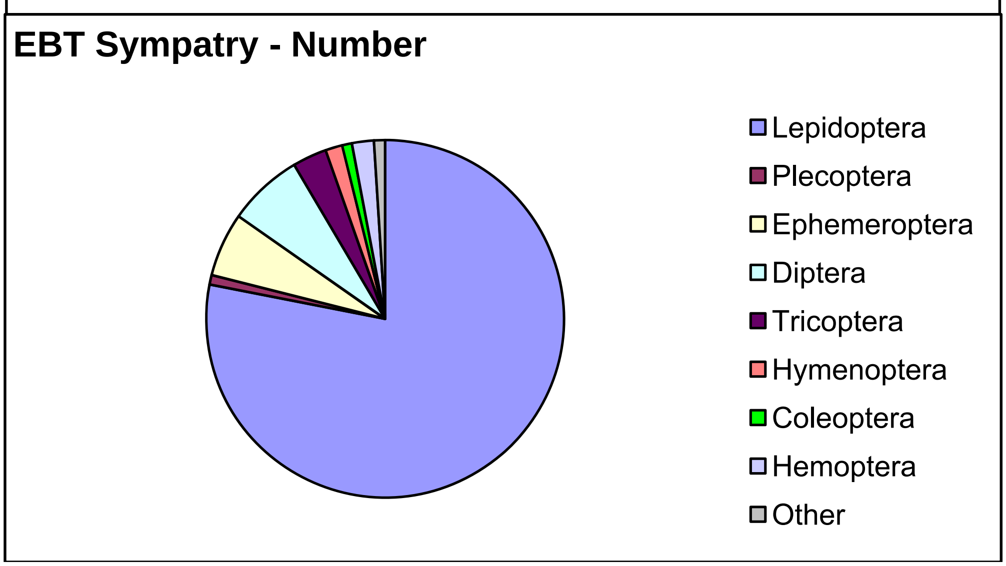


Figure 13. Proportion of the number of food items by Order in westslope cutthroat trout (WCT) and brook trout (EBT) stomachs in Muskrat Creek.

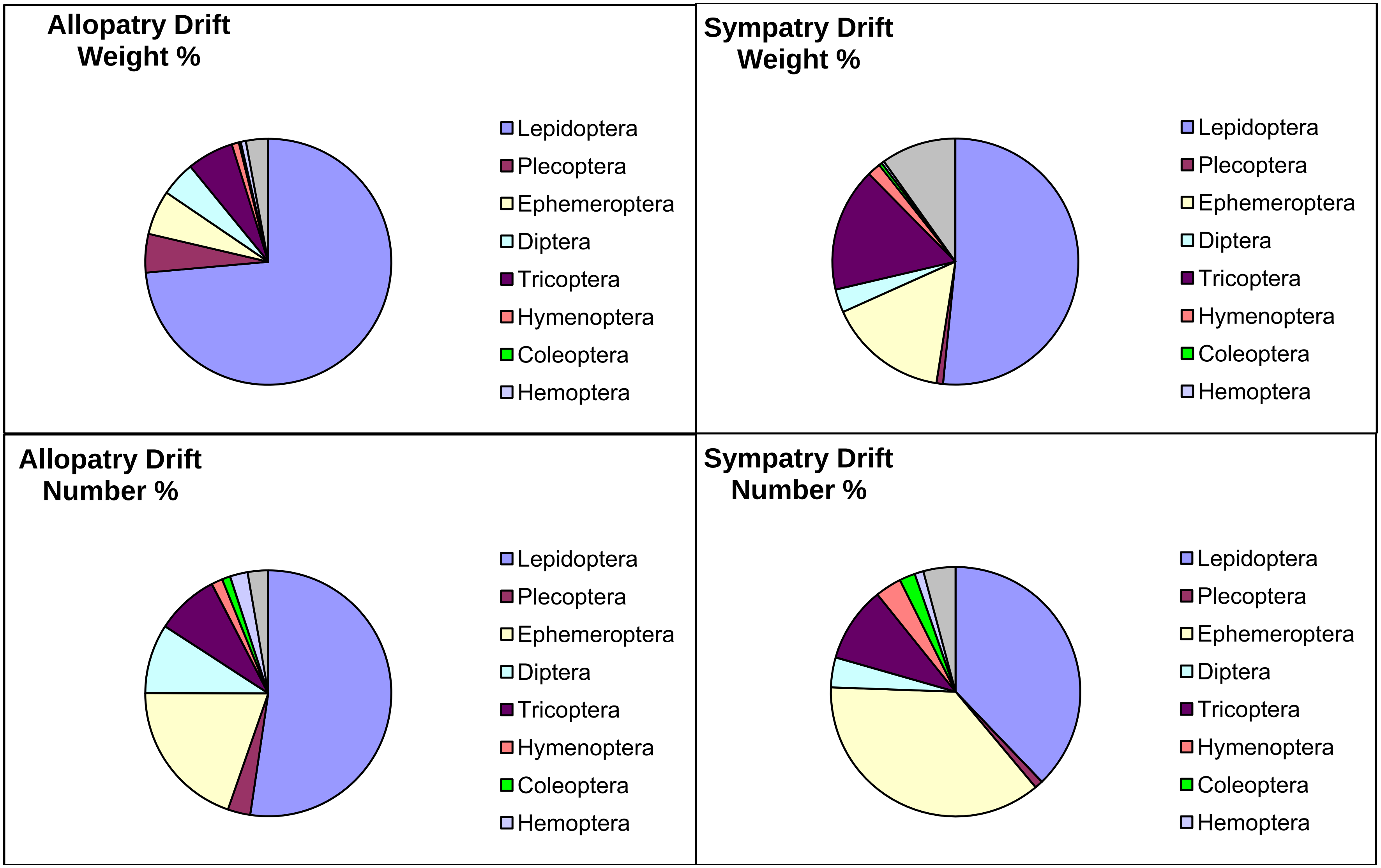
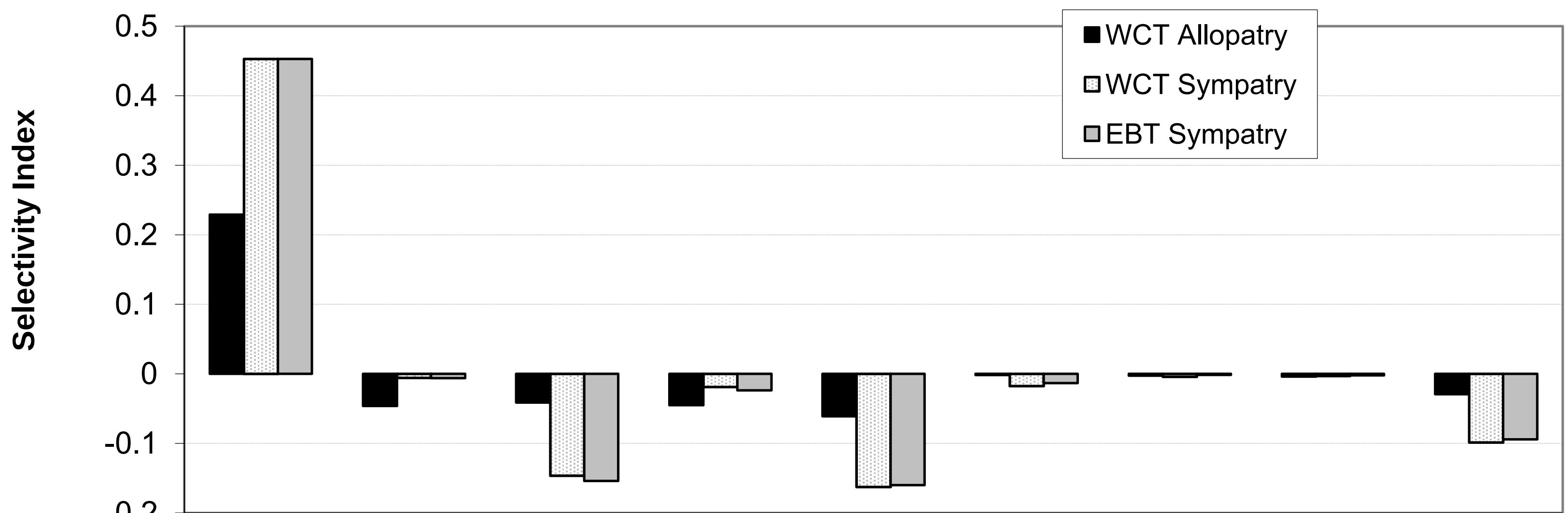


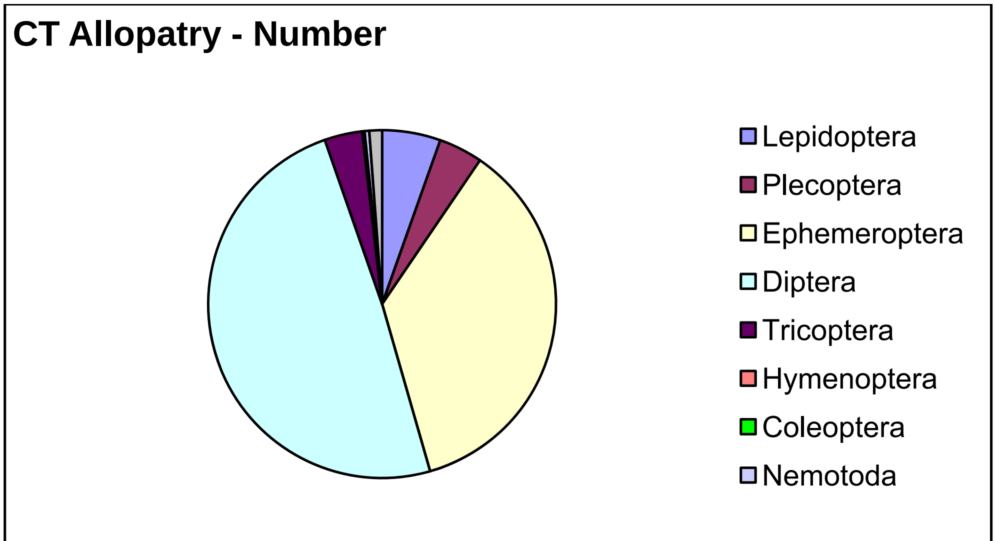
Figure 14. Proportion of drifting organisms by weight (top graphs) and number (bottom graphs) in a reach of Muskrat Creek where westslope cutthroat occur in allopatry (left graphs) and in sympatry with brook trout (right graphs).

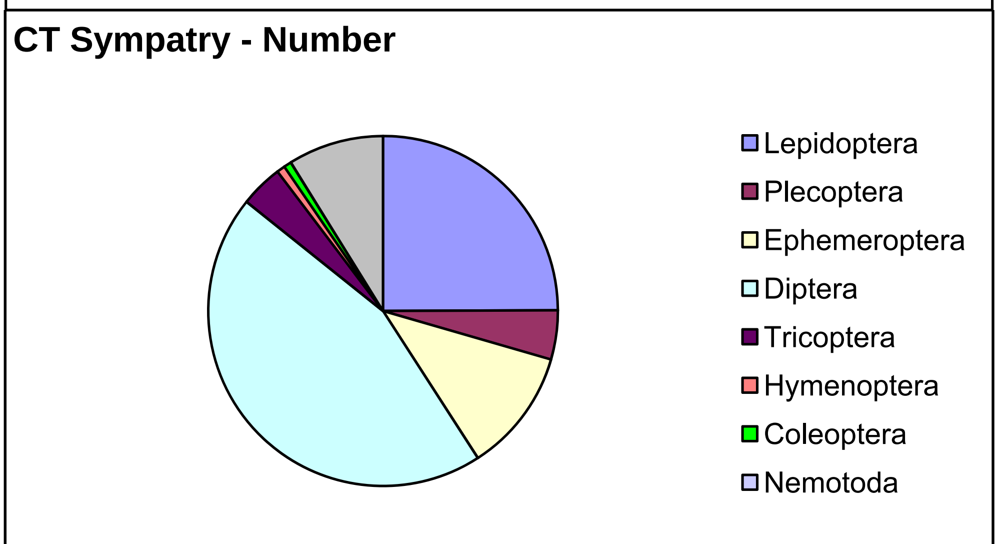
Muskrat Creek Selectivity by Weight



	Lepidoptera	Plecoptera	Ephemeroptera	Diptera	Tricoptera	Hymenoptera	Coleoptera	Hemoptera	Other
WCT Allopatry	0.228943432	-0.046162451	-0.04131655	-0.045000083	-0.061107979	-0.001782165	-0.002571167	-0.003965031	-0.029294324
WCT Sympatry	0.452857115	-0.005734569	-0.146527754	-0.018775275	-0.162627826	-0.017465686	-0.004202124	-0.003000245	-0.098573831
EBT Sympatry	0.452969554	-0.006063945	-0.154083231	-0.023692215	-0.160053846	-0.013241421	-0.001408316	-0.002209507	-0.09410068

Figure 15. Food item selection by westslope cutthroat trout in allopatry, westslope cutthroat trout in sympatry with brook trout, and brook trout by Order for fish sampled in Muskrat Creek. Positive values indicate selection, negative values indicate avoidance, and values near zero indicate items were taken in proportion to availability.





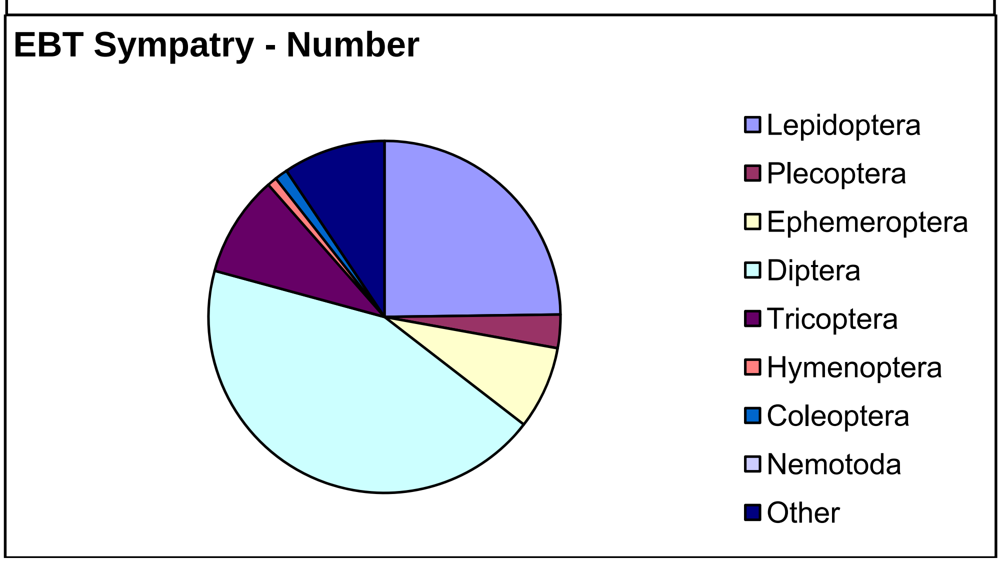


Figure 16. Proportion of the number of food items by Order in westslope cutthroat trout (CT) and brook trout (EBT) stomachs in Whites Creek.

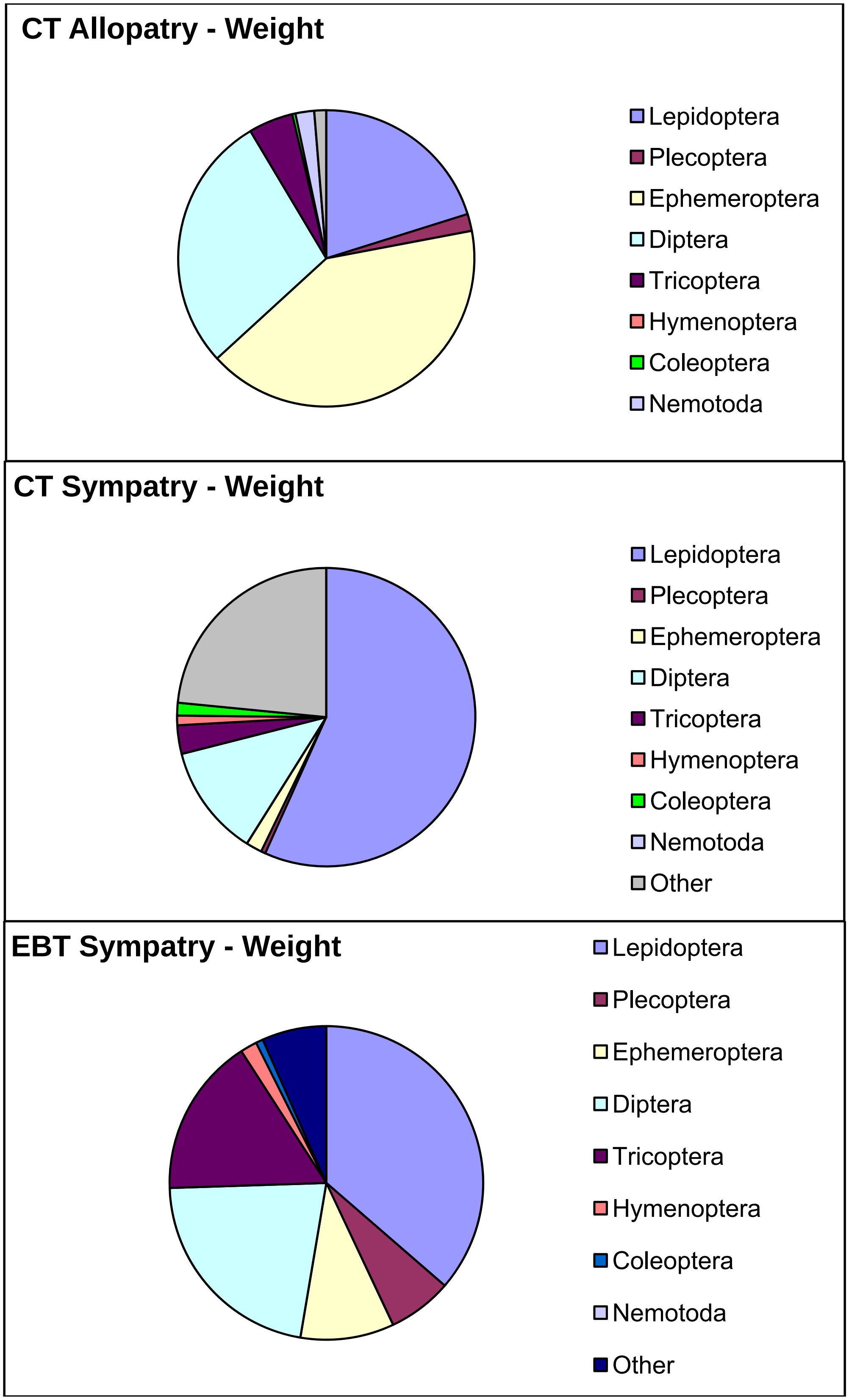


Figure 17. Proportion of the weight of food items by Order in westslope cutthroat trout (WCT) and brook trout (EBT) stomachs in Whites Creek.

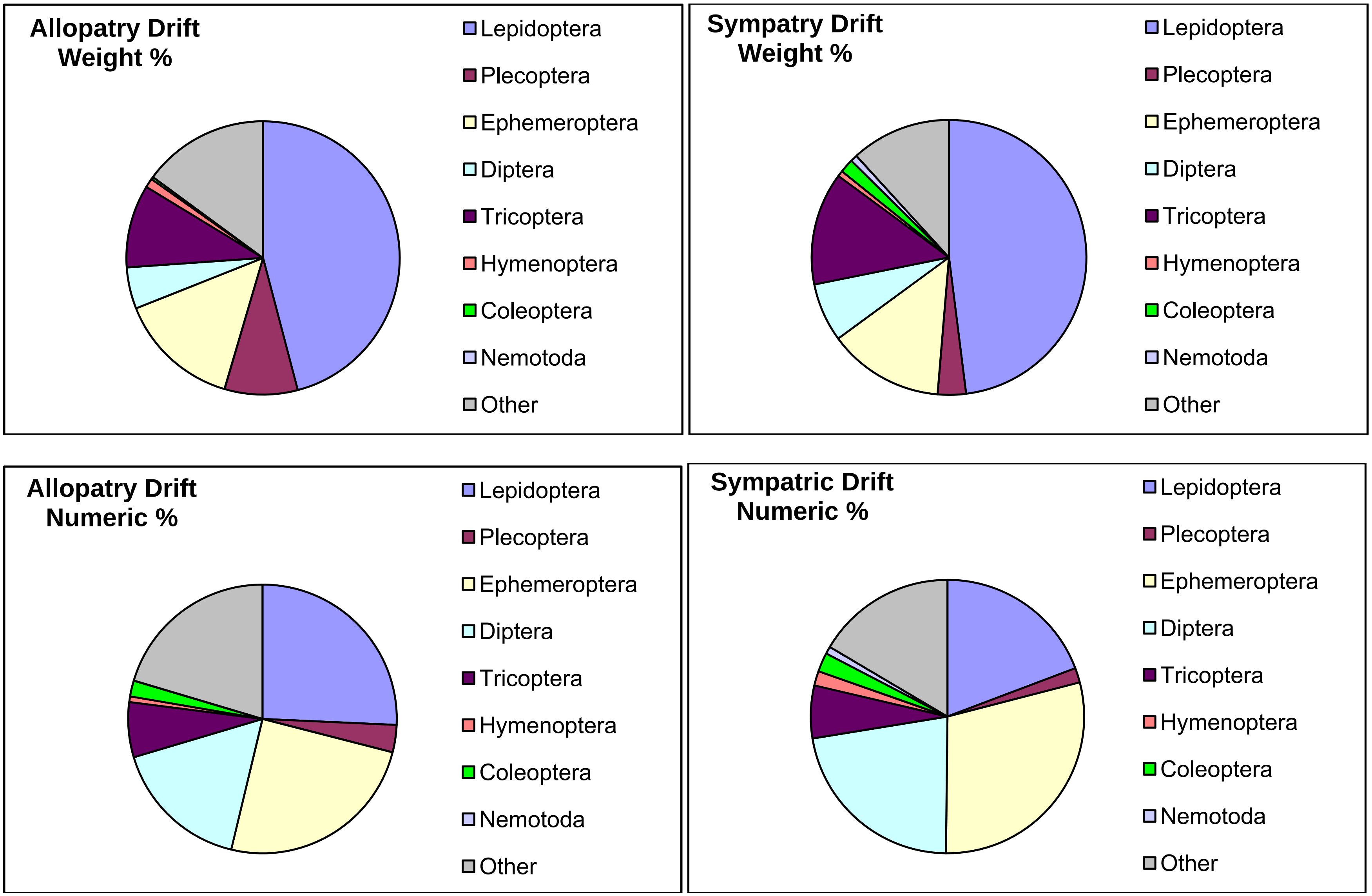
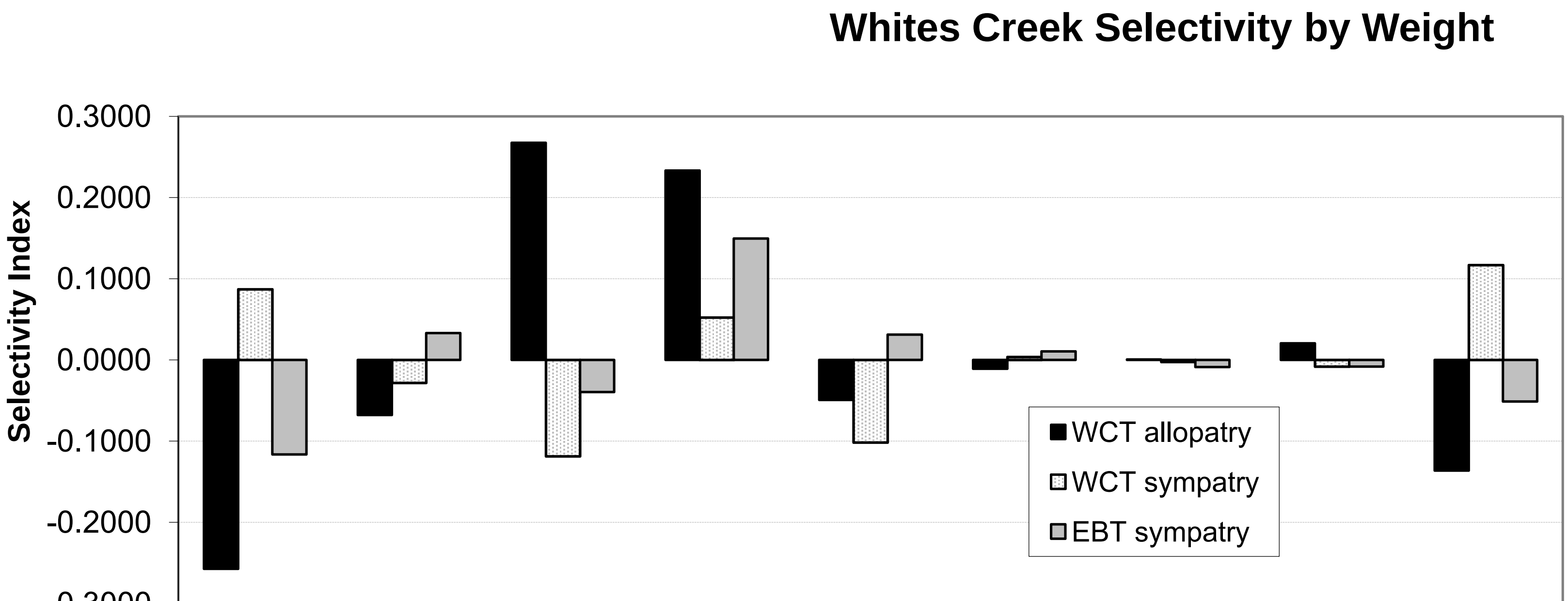


Figure 18. Proportion of drifting organisms by weight (top graphs) and number (bottom graphs) in a reach of Whites Creek where westslope cutthroat occur in allopatry (left graphs) and in sympatry with brook trout (right graphs).



	Lepidoptera	Plecoptera	Ephemeroptera	Diptera	Tricoptera	Hymenoptera	Coleoptera	Nemotoda	Other
WCT allopatry	-0.2574	-0.0680	0.2675	0.2332	-0.0493	-0.0109	0.0006	0.0205	-0.1363
WCT sympatry	0.0870	-0.0284	-0.1187	0.0522	-0.1018	0.0036	-0.0025	-0.0083	0.1168
EBT sympatry	-0.1165	0.0332	-0.0396	0.1494	0.0312	0.0105	-0.0088	-0.0083	-0.0512

Figure 19. Food item selection by westslope cutthroat trout in allopatry, westslope cutthroat trout in sympatry with brook trout, and brook trout by Order for fish sampled in Whites Creek. Positive values indicate selection, negative values indicate avoidance, and values near zero indicate items were taken in proportion to availability.

Discussion

Response of Westslope Cutthroat Trout to Removal of Brook Trout

Results from this study suggest that 75 mm and longer brook trout and WCT occupied similar niches in these three streams. Standing crops of WCT in allopatry equaled or exceeded levels estimated for brook and WCT in sympatry following the removal of brook trout from treatment reaches within all three streams. We suspect that cutthroat trout populations in Muskrat Creek would have rebounded faster if we had not trans-located a large proportion of this population to the upper drainage; however, we monitored this population's recovery over a long enough time to observe their total recovery in the treatment reach. While the competitive mechanisms that allow brook trout to displace WCT are still in question, our results suggest that densities of juvenile brook trout suppressed both individual body condition and densities of juvenile WCT. We obtained concordant results from three separate analyses indicating that interspecific competition between juvenile brook trout and cutthroat trout may be almost as strong as intraspecific competition among juvenile cutthroat trout (Tables 5 and 7). Our results provide additional evidence to support previous inferences made by several researchers that competition is a more likely mechanism for displacement of cutthroat trout by brook trout than predation (McGrath and Lewis 2007) and that this competition likely occurs at young ages (Novinger 2000; Shepard et al. 2002; Peterson et al. 2004; Hilderbrand 2003; McGrath and Lewis 2007).

It is possible that competitive effects could be even more pronounced between age-0 brook trout and cutthroat trout (Novinger 2000; Shepard et al. 2003; Peterson et al. 2004; Hilderbrand 2003; McGrath and Lewis 2007; however, see Koenig 2006 who suggests competition is most pronounced at age-1). Unfortunately, we could not estimate abundance or condition of age-0 WCT during this study due to their extremely small size (often < 50 mm at the end of their first summer), our concerns about unacceptable mortality on these fry during sampling, and the large numbers of fish that were captured and processed during brook trout removal efforts. Despite this shortcoming, we have strong evidence that brook trout effectively compete with juvenile cutthroat trout.

The significant and positive correlation between body conditions of adult and juvenile WCT, along with the significant and negative correlation between juvenile WCT abundance and body condition of adult WCT (Table 5), suggests that during good years both juvenile and adult WCT have good body conditions and that intraspecific competition may be manifested by adult cutthroat trout suppressing densities of juvenile cutthroat trout. This finding lends support to the self-thinning hypothesis, which other researchers have also documented for stream-resident salmonids (Bohlin et al. 1994; Dunham and Vinyard 1997).

We did not observe any significant differences in the effect of brook versus cutthroat trout on condition factors of individual age-1 and older cutthroat trout, despite testing a relatively wide range of densities and sizes for stream-resident forms of each species. This suggests that interspecific competition between age-1 and older brook trout and cutthroat trout may be nearly the same as intraspecific competition between age-1 and older cutthroat trout. We found that breadth of competition was significant in both Whites and Muskrat creeks, but that breadth of competition was not significantly different between the two species. This finding indicates that similar-sized fish compete with each other, regardless of species. We did not test for species-asymmetric competition as we did not test effects of cutthroat trout on brook trout by removing cutthroat trout from any systems. Several studies (e.g. McGrath and Lewis 2007; McHugh and Budy 2006; McHugh et al. 2008; Shemai et al. 2007) and our observations indicate that there is likely a strong species-asymmetry in competition effects between nonnative salmonids and cutthroat trout with nonnative salmonids displacing cutthroat trout wherever abiotic conditions allow these nonnative species to invade (Fausch 2007). Species-asymmetry has also been observed among co-occurring native species (Jonsson et al. 2008).

In White's Creek we did not find any evidence for size-asymmetric competition, but we did find evidence for it in Muskrat Creek. We are uncertain why we observed this difference, but we speculate it could be related to the difference in the physical characteristics of these two streams. Whites Creek is a smaller stream with a long intermittent reach of stream above our sample area that seldom flows. It may be that larger trout in Whites Creek do not accrue any additional benefits for their larger size due to relatively small habitats that are isolated at both the upstream and downstream boundaries. Conversely, Muskrat Creek is a larger stream where larger trout may accrue additional benefits with their larger size. Case (2000; p. 315) concluded, "…the outcome of competition depends upon environmental conditions and sometimes on the initial conditions." We agree and our results support this conclusion.

As mentioned above, competition may be even stronger when fish are age-0 and size-asymmetry of age-0 fish likely plays a role in outcomes of this competition. Young (2003) observed that for coho salmon (*O. kistuch*) and steelhead trout (*O. mykiss*) larger age-0 individuals dominated smaller age-0 individuals with larger individuals adopting aggressive, and smaller individuals adopting passive, fighting behaviors. In a later paper Young (2004) concluded that because coho fry emerged earlier and maintained a size advantage over steelhead fry, interspecific competition was strongly asymmetrical, in favor of coho, and that habitat selection by both species was strongly dependent upon densities of coho fry. We suggest that this mechanism probably explains the commonly reported dominance of age-0 brook trout over age-0 cutthroat trout (Griffith 1974) and may be a major factor responsible for the displacement of cutthroat trout by brook trout.

Evaluation of Habitat Restoration

Unfortunately, we were unable to evaluate the role of instream cover on densities or condition factors of cutthroat trout and brook torut as rigorously as we had planned because our study design was not implemented during habitat restoration projects due to logistical constraints. We found that rigorous evaluations will require funding of not only monitoring and evaluation of restoration projects, but also funding of the habitat restoration projects to ensure restoration treatments follow the study design. Our results suggest that while habitat restoration projects may increase total densities of trout, their effects on individual species vary and in some cases these projects may be increasing densities of brook trout more than cutthroat trout, while in other cases the opposite appears to occur. We suggest these differences need further research and causal mechanisms need to be better defined.

Comparative Food Habitats

Our study of the food habits of age-2 and older cutthroat and brook trout indicated that there were some differences in food consumed by cutthroat trout in allopatry versus those in sympatry with brook trout. While this study was somewhat confounded by the extremely high abundances of adult terrestrial budworms, results indicated that cutthroat trout in allopatry fed more heavily on Ephemeropterans than cutthroat trout in sympatry with brook trout. Cutthroat trout in sympatry with brook trout fed more on terrestrial adults than cutthroat trout in allopatry. We suggest that this might be occurring because benthic oriented brook trout are displacing cutthroat trout from deeper sites (space competition) that force cutthroat trout out of these deeper water habitats to positions closer to the water's surface where terrestrial budworm adults were more easily available to them. If this is true, this type of competition may have important implications in making older cutthroat trout more vulnerable to avian and mammalian predators.

Acknowledgements

Montana Fish, Wildlife and Parks was funded through the State Wildlife Grant Program. The Wild Fish Habitat Initiative administered through the Montana State University Water Center also funded this project. We thank Gretchen Rupp and the staff at the Water Center for their support. B. Shepard also received support from a National Science Foundation grant and the Eugene Maughan Graduate Student Scholarship from the Western Division of the American Fisheries Society. Dr. Al Zale of USGS Montana Cooperative Fishery Research Unit, MSU, and Dr. Mark Taper of the Ecology Department of MSU also helped review this report. Biologists and field workers from Montana Fish, Wildlife and Parks, the USDA Forest Service (Lewis and Clark, Beaverhead-Deerlodge, and Helena National Forests), and the USDI Bureau of Land Management provided logistic support and assisted with fieldwork, including removal of brook trout. We especially wish to thank biologists L. Nelson, D. Moser, R. Spoon, M. Enk, J. Brammer, and A. Harper, and field workers J. Jones, J. Ferguson, C. Downs, S. Ireland, D. Fuller, B. Bailey, D. Barnes, K. Duffy, D. Irlbeck, M. Sloat, M. Norberg, A. Sanhow, D. Staples, D. Pearson, L. Renner, B. Heser, and C. Thurner. L. Renner and D. Pearson picked drift net and stomach samples, made preliminary identifications of each item, counted and weighed these samples by Order, and conducted initial data analyses. D. Irlbeck also assisted with initial food habits data analyses. Dr. Dan

Gustafsen (aquatic species) and Dr. Mike Ivie (terrestrial adults) of Montana State University verified our identification of food and drift organisms.

References

Adams, S. B. 1999. Mechanisms limiting a vertebrate invasion: brook trout in mountain streams of the northwestern USA. Doctoral dissertation, University of Montana, Missoula, Montana.

Adams, S. B., C. A. Frissell, and B. E. Rieman. 2000. Movements of nonnative brook trout in relation to stream channel slope. Transactions of the American FisheriesSociety 129:623-638.

Adams, S. B., C. A. Frissell, and B. E. Rieman. 2001. Geography of invasion in mountain streams: consequences of headwater lake fish introductions. Ecosystems 4:296-307.

Adams, S. B., C. A. Frissell, and B. E. Rieman. 2002. Changes in distribution of nonnative brook trout in an Idaho drainage over two decades. Transactions of the American Fisheries Society 131:561-568.

Allen, G. H. and L. G. Claussen. 1960. Selectivity of food by brook trout in a Wyoming beaver pond. Transactions of the American Fisheries Society 89:80-81.

Allendorf, F. W. and R. F. Leary. 1988. Conservation and distribution of genetic variation in a polytypic species, the cutthroat trout. Conservation Biology 2:170-184.

Anderson, R. O. and S. J. Gutreuter. 1983. Length, weight, and associated structural indices. Pages 283-300 in L. A. Nielsen and D. L. Johnson, editors. Fisheries Techniques. American Fisheries Society, Bethesda, Maryland.

Angers, B., L. Bernatchez, A. Angers, and L. Desgroseillers. 1995. Specific microsatellite loci for brook charr reveal strong population subdivision on a microgeographic scale. Journal of Fish Biology 47:177-185.

Arthington, A. H. 1991. Ecological and genetic impacts of introduced and translocated freshwater fishes in Australia. Canadian Journal of Fisheries and Aquatic Sciences 48(Supplement 1):33-43.

Ball, O. P. and O. B. Cope. 1961. Mortality studies on cutthroat trout in Yellowstone Lake. Research Report 55, U.S. Department of Interior, Fish and Wildlife Service, Washington, D.C.

Barrineau, C. E., W. A. Hubert, P. D. Dey, and T. C. Annear. 2005. Winter ice processes and pool habitat associated with two types of constructed instream structures. North American Journal of Fisheries Management 25:1022-1033.

Beauchamp, D. A., D. J. Stewart, and G. L. Thomas. 1989. Corroboration of a bioenergetics model for sockeye salmon. Transactions of the American Fisheries Society 118:597-607.

Behnke, R. J. 1979. Monograph of the native trouts of the genus *Salmo* of Western North America. Final report under contract to USDI Bureau of Land Management and Fish and Wildlife Service, and USDA Forest Service, Region 2, Lakewood, Colorado.

Behnke, R. J. 1992. Native trout of Western North America. American Fisheries Society, Monograph 6, Bethesda, Maryland.

Belanger, G. and M. A. Rodriguez. 2001. Homing behaviour of stream-dwelling brook charr following experimental displacement. Journal of Fish Biology 59:987-1001.

Benjamin, J. R. 2006. Invasion by nonnative brook trout in Panther Creek, Idaho: roles of habitat quality, connectivity, and biotic resistance. Master's thesis. Boise State University, Boise, Idaho.

Benjamin, J. R., J. B. Dunham, and M. R. Dare. 2007. Invasion by nonnative brook trout in Panther Creek, Idaho: roles of local habitat quality, biotic resistance, and connectivity to source habitats. Transactions of the American Fisheries Society 136:875-888.

Binns, N. A. and R. Remmick. 1994. Response of Bonneville cutthroat trout and their habitat to drainage-wide habitat management at Huff Creek, Wyoming. North American Journal of Fisheries Management 14:669-680.

Bjornn, T. C. and D. W. Reiser. 1991. Habitat requirements of salmonids in streams. Pages 83-138 *in* Meehan, W. R., editor. Influences of forest and rangeland mangement on salmonid fishes and their habitats. Special Publication 19. American Fisheries Society, Bethesda, Maryland.

Bjornn, T. C. and G. A. Liknes. 1986. Life history, status, and management of westslope cutthroat trout. Pages 57-46 *in* J. S. Griffith, editor. The ecology and management of interior stocks of cutthroat trout. Special Publication of the Western Division, American Fisheries Society, Bethesda, Maryland.

Bohlin, T., C. Dellefors, U. Faremo, and A. Johlander. 1994. The energetic equivalence hypothesis and the relation between population-density and body-size in stream-living salmonids. American Naturalist 143:478-493.

Bohn, T., and P.A. Amundsen. 2001. The competitive edge of an invading specialist. Ecology 82:2150-2163.

Bozek, M. A. and W. A. Hubert. 1992. Segregation of resident trout in streams as predicted by three habitat dimensions. Canadian Journal of Zoology 70:886–890.

Brown, C. J. D. 1971. Fishes of Montana. Montana University Press, Bozeman, Montana.

Burger, J. C., M. A. Patten, T. R. Prentice, and R. A. Redak. 2001. Evidence for spider community resilience to invasion by non-native spiders. Biological Conservation 98:241-249.

Burton, G. W. and E. P. Odum. 1945. The distribution of stream fish in the vicinity of Mountain Lake, Virginia. Ecology 26:182-194.

Byers, J. E. 2000. Competition between two estuarine snails: implications for invasions of exotic species. Ecology 81:1225-1239.

Byers, J. E. and E. G. Noonburg. 2003. Scale dependent effects of biotic resistance to biological invasion. Ecology 84:1428-1433.

Cambray, J. A. 2003. Impact on indigenous species biodiversity caused by the globalisation of alien recreational freshwater fisheries. Hydrobiologia 500:217-230.

Case, T. J. 1996. Global patterns in the establishment and distribution of exotic birds. Biological Conservation 78:69-96.

Case, T. J. 2000. An illustrated guide to theoretical ecology. Oxford University Press, New York, New York, USA.

Cegelski, C. C., M. R. Campbell, K. A. Meyer, and M. S. Powell. 2006. Multiscale genetic structure of Yellowstone cutthroat trout in the Upper Snake River Basin. Transactions of the American Fisheries Society 135:711-726.

Collen, P. and R. J. Gibson. 2001. The general ecology of beavers (*Castor* spp.), as related to their influence on stream ecosystems and riparian habitats, and the subsequent effects on fish - a review. Reviews in Fish Biology and Fisheries 10:439-461.

Crowder, L. B. 1990. Community ecology. Pages 609-632 *in* C. B. Schreck and P. B. Moyle, editors. Methods for fish biology. American Fisheries Society, Bethesda, Maryland.

Cummings, T. R. 1987. Brook trout competition with greenback cutthroat trout in Hidden Creek, Colorado. Master's thesis, Colorado State University, Fort Collins, Colorado.

D'Antonio, C. M. and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass fire cycle, and global change. Annual Review of Ecology and Systematics 23:63-87.

DeRito, J. N. 2004. Assessment of reproductive isolation between Yellowstone cutthroat trout and rainbow trout in the Yellowstone River, Montana. Montana State University, Bozeman, Montana.

DeStaso, J., III and F. J. Rahel. 1994. Influence of water temperature on interactions between juvenile Colorado River cutthroat trout and brook trout in a laboratory stream. Transactions of the American Fisheries Society 123:289-297.

Donald, D. B., R. S. Anderson, and D. W. Mayhood. 1980. Correlations between brook trout growth and environmental variables for mountain lakes in Alberta. Transactions of the American Fisheries Society 109:603-610.

Downs, C. C., R. G. White, and B. B. Shepard. 1997. Age at sexual maturity, sex ratio, fecundity, and longevity of isolated headwater populations of westslope cutthroat trout. North American Journal of Fisheries Management 17:85-92.

Dunham, J. B., D. S. Pilliod, and M. K. Young. 2004. Assessing the consequences of nonnative trout in headwater ecosystems in western North America. Fisheries 29:18-+.

Dunham, J. B., M. M. Peacock, B. E. Rieman, R. E. Schroeter, and G. L. Vinyard. 1999. Geographic variability in the distribution of stream-living Lahontan cutthroat trout. Transactions of the American Fisheries Society 128:875-889.

Dunham, J. B., M. E. Rahn, R. E. Schroeter, and S. W. Breck. 2000. Diets of sympatric Lahontan cutthroat trout and nonnative brook trout: implications for species interactions. Western North American Naturalist 60:304-310.

Dunham, J. B., S. B. Adams, R. E. Schroeter, and D. C. Novinger. 2002. Alien invasions in aquatic ecosystems: toward an understanding of brook trout invasions and potential impacts on inland cutthroat trout in western North America. Reviews in Fish Biology and Fisheries 12:373–391.

Dunham, J., B. Rieman, and G. Chandler. 2003. Influences of temperature and environmental variables on the distribution of bull trout within streams at the southern margin of its range. North American Journal of Fisheries Management 23:894-904.

Dunham, J. B. and G. L. Vinyard. 1997. Relationship between body mass, population density, and the self-thinning rule in stream-living salmonids. Canadian Journal of Fisheries and Aquatic Sciences 54:1025-1030.

Dwyer, W. P., B. B. Shepard, and R. G. White . 2001. Effect of backpack electroshock on westslope cutthroat trout injury and growth 110 and 250 days posttreatment. North American Journal of Fisheries Management 21:646-650.

Elton, C. S. 1958. The ecology of invasions by animals and plants. Harvard University Press, Cambridge, Massachusetts.

Erman, D. C. 1986. Long-term structure of fish populations in Sagehen Creek, California. Transactions of the American Fisheries Society 115:682-692.

Fausch, K. D. 1988. Tests of competition between native and introduced salmonids in streams: What have we learned? Canadian Journal of Fisheries and Aquatic Science 45:2238-2246.

Fausch, K. D. 1989. Do gradient and temperature affect distribution of, and interactions between juvenile brook char and other salmonids in streams? Physiological Ecology of Japan, Special Volume 1:303–322.

Fausch, K. D. 2007. Introduction, establishment and effects of non-native salmonids: considering the risk of rainbow trout invasion in the United Kingdom. Journal of Fish Biology 71:1-32.

Fausch, K. D., C. L. Hawkes, and M. G. Parsons. 1988. Models that predict standing crop of stream fish from habitat variables: 1950-85. General Technical Report PNW-GTR-213, USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Fechhelm, R. G., R. E. Dillinger, Jr., B. J. Gallaway, and W. B. Griffiths. 1992. Modeling of in situ temperature and growth relationships for yearling broad whitefish in Prudhoe Bay, Alaska. Transactions of the American Fisheries Society 121:1-12.

Flick, W. A. and D. A. Webster. 1975. Movement, growth, and survival in a stream population of wild brook trout (*Salvelinus fontinalis*) during a period of removal of non-trout species. Journal of the Fisheries Research Board of Canada 32:1359-1367.

Forseth, T., M. A. Hurley, A. J. Jensen, and J. M. Elliott. 2001. Functional models for growth and food consumption of Atlantic salmon parr, *Salmo salar*, from a Norwegian river. Freshwater Biology 46:173-186.

Franco, E. A. D. and P. Budy. 2005. Effects of biotic and abiotic factors on the distribution of trout and salmon along a longitudinal stream gradient. Environmental Biology of Fishes 72:379-391.

Frissell, C. A., W. J. Liss, C. E. Warren, and M. D. Hurley. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environmental Management 10:199-214.

Fuller, P. A. M. L., L. E. O. Nico G., and Williams James D. 1999. Nonindigenous fishes introduced into inland waters of the United States. Special Publication 27, American Fisheries Society, Bethesda, Maryland.

Gido, K. B., J. F. Schaefer, and J. Pigg. 2004. Patterns of fish invasions in the Great Plains of North America. Biological Conservation 118:121-131.

Gowan, C. and K. D. Fausch. 1996. Mobile brook trout in two high-elevation Colorado streams: re-evaluating the concept of restricted movement. Canadian Journal of Fisheries and Aquatic Sciences 53:1370-1381.

Gresswell, R. E. 1988. Status and management of interior stocks of cutthroat trout. American Fisheries Society Symposium 4.

Gresswell, R. E. 1995. Yellowstone cutthroat trout. Pages 36-54 *in* Young, M. K., Technical Editor. Conservation assessment for inland cutthroat trout, USDA, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

Gresswell, R. E. 1997. Introduction to ecology and management of potamodromous salmonids. North American Journal of Fisheries Management 17:1027-1028.

Griffith, J. S. 1970. Interaction of brook trout and cutthroat trout in small streams. Doctoral dissertation, University of Idaho, Moscow, Idaho.

Griffith, J. S. 1972. Comparative behavior and habitat utilization of brook trout (*Salvelinus fontinalis*) and cutthroat trout (*Salmo clarki*) in small streams in northern Idaho. Journal of the Fisheries Research Board of Canada 29:265-273.

Griffith J.S. 1974. Utilization of invertebrate drift by brook trout (*Salvelinus fontinalis*) and cutthroat trout (*Salmo clarki*) in small streams in Idaho. Transactions of the American Fisheries Society 103:440-447.

Griffith, J. S. 1988. Review of competition between cutthroat trout and other salmonids. Pages 134-140 *in* Gresswell, R. E., editor. Status and management of interior stocks of cutthroat trout. American Fisheries Society, Bethesda, Maryland.

Grosholz, E. D. and G. M. Ruiz. 1996. Predicting the impact of introduced marine species: lessons from the multiple invasions of the European green crab *Carcinus maenas*. Biological Conservation 78:59-66.

Hadley, K. Status report on the Yellowstone cutthroat trout (*Salmo clarki bouvieri*) in Montana. Final report submitted to Montana, Department of Fish, Wildlife and Parks, Fisheries Division, Helena, Montana.

Hanzel, D. A. 1959. The distribution of the cutthroat trout (*Salmo clarki*) in Montana. Proceedings of the Montana Academy of Sciences 19:32-71.

Hayes, J. W., J. D. Stark, and K. A. Shearer. 2000. Development and test of a whole-lifetime foraging and bioenergetics growth model for drift-feeding brown trout. Transactions of the American Fisheries Society 129:315-332.

Hicks, B. J., J. D. Hall, and P. A. Bisson. 1991. Responses of salmonids to habitat changes. Pages 483-518 *in* Meehan, W. R., editor. Influences of forest and rangeland mangement on salmonid fishes and their habitats. Special Publication 19. American Fisheries Society, Bethesda, Maryland.

Hawkins, C. P., J. L. Kershner, P. A. Bisson, M. D. Bryant, L. M. Decker, S. V. Gregory, D. A. McCullough, C. K. Overton, G. H. Reeves, R. J. Steedman, and M. K. Young. 1993. A hierarchical approach to classifying stream habitat features. Fisheries 18:3-12.

Hilderbrand, R. H. 2003. The roles of carrying capacity, immigration, and population synchrony on persistence of stream-resident cutthroat trout. Biological Conservation 110:257-266.

Hilderbrand, R. H. and J. L. Kershner. 2000. Conserving inland cutthroat trout in small streams: how much stream is enough? Fisheries 20:513-520.

Irving, R. B. 1954. Ecology of the cutthroat trout in Henrys Lake, Idaho. Transactions of the American Fisheries Society 84:275-296.

Jakober, M. J., T. E. McMahon, R. F. Thurow, and C. G. Clancy. 1998. Role of stream ice on fall and winter movements and habitat use by bull trout and cutthroat trout in Montana headwater streams. Transactions of the American Fisheries Society 127:223-235.

Johnson, H. E. 1963. Observations on the life history and movement of cutthroat trout, Salmo clarki, in Flathead River drainage, Montana. Proceedings of the Montana Academy of Sciences 23: 96-110.

Johnson, S. L., F. J. Rahel, and W. A. Hubert. 1992. Factors influencing the size structure of brook trout populations in beaver ponds in Wyoming. North American Journal of Fisheries Management 12:118-124.

Jonsson, B., K. Hindar, and T. Northcote. 1984. Optimal age at sexual maturity of sympatric and experimentally allopatric cutthroat trout and Dolly Varden charr. Oecologia 61: 319-325.

Kennedy, B. M., D. P. Peterson, and K. D. Fausch. 2003. Different life histories of brook trout populations invading mid-elevation and high-elevation cutthroat trout streams in Colorado. Western North American Naturalist 63:215-223.

Koenig, M. K. 2006. Habitat and biotic factors influencing the distribution and recruitment of juvenile cutthroat trout in the Teton River, Idaho. Master's thesis, Utah State University, Logan, Utah.

Kolar, C. S. and D. M. Lodge. 2001. Progress in invasion biology: predicting invaders. Trends in Ecology & Evolution 16:199-204.

Kondolf, G. M., M. W. Smeltzer, and S. F. Railsback. 2001. Design and performance of a channel reconstruction project in a coastal California gravel-bed stream. Environmental Management 28:761-776.

Krueger, C. C. and B. May. 1991. Ecological and genetic effects of salmonid introductions in North America. Canadian Journal of Fisheries and Aquatic Sciences 48:66-77.

Kruse, C. G., W. A. Hubert, and F. J. Rahel. 2000. Status of Yellowstone cutthroat trout in Wyoming waters. Fisheries 20:693-705.

Lambrinos, J. G. 2004. How interactions between ecology and evolution influence contemporary invasion dynamics. Ecology 85:2061-2070.

Laurance, W. F. 1997. A distributional survey and habitat model for the endangered northern bettong *Bettongia tropica* in tropical Queensland. Biological Conservation 82:47-60.

Leyse, K. E., S. P. Lawler, and T. Strange. 2004. Effects of an alien fish, Gambusia affinis, on an endemic California fairy shrimp, *Linderiella occidentalis*: implications for conservation of diversity in fishless waters. Biological Conservation 118:57-65.

Light, R. W., P. H. Adler, and D. E. Arnold. 1983. Evaluation of gastric lavage for stomach analyses. North American Journal of Fisheries Management 3:81-85.

Liknes, G. A. and P. J. Graham. 1988. Westslope cutthroat trout in Montana: life history, status, and management. Pages 53-60 *in* R. E. Gresswell. Status and management of interior stocks of cutthroat trout. American Fisheries Society, Bethesda, Maryland.

Lindstrom, J. W. and W. A. Hubert. 2004. Ice processes affect habitat use and movements of adult cutthroat trout and brook trout in a Wyoming foothills stream. North American Journal of Fisheries Management 24:1341-1352.

Lisle, T. E. 1987. Using "residual depths" to monitor pool depths independently of discharge. Research Note PSW-394, USDA Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkeley, California.

Lukens, J. R. 1978. Abundance, movements and age structure of adfluvial westslope cutthroat trout in the Wolf Lodge Creek drainage, Idaho. Master's thesis, University of Idaho, Moscow, Idaho.

MacPhee, C. 1966. Influence of differential angling mortality and stream gradient on fish abundance in a trout-sculpin biotope. Transactions of the American Fisheries Society 95:381-387.

MacCrimmon, H. R. and J. S. Campbell. 1969. World distribution of brook trout, *Salvelinus fontinalis*. Journal of the Fisheries Research Board of Canada 26:1699-1725.

Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecological Applications 10:689-710.

Marchetti, M. P., T. Light, P. B. Moyle, and J. H. Viers. 2004. Fish invasions in California watersheds: testing hypotheses using landscape patterns. Ecological Applications 14:1507-1525.
Salmo trutta

Marchetti, M. P., J. L. Lockwood, and T. Light. 2006. Effects of urbanization on California's fish diversity: differentiation, homogenization and the influence of spatial scale. Biological Conservation 127:310-318.

May, B. E., W. Urie, and B. B. Shepard. 2003. Range-wide status of Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*): 2001. Bozeman, Montana, USDA Forest Service, Gallatin National Forest.

McGrath, C. C. 2004. Trophic roles of native greenback cutthroat trout and non-native brook trout in montane streams of Colorado. Doctoral dissertation, University of Colorado, Boulder, Colorado.

McGrath, C. C. and W. M. Lewis, Jr. 2007. Competition and predation as mechanisms for displacement of greenback cutthroat trout by brook trout. Transactions of the American Fisheries Society 136:1381-1392.

McHugh, P. and P. Budy. 2006. Experimental effects of nonnative brown trout on the individual- and population-level performance of native Bonneville cutthroat trout. Transactions of the American Fisheries Society 135:1441-1455.

McHugh, P., P. Budy, G. Thiede, and E. Vandyke. 2008. Trophic relationships of nonnative brown trout, , and native Bonneville cutthroat trout, *Oncorhynchus clarkii utah*, in a Northern Utah, USA river. Environmental Biology of Fishes 81:63-75.

McIntyre, J. D. and B. E. Rieman. 1995. Westslope cutthroat trout. Pages 1-15 *in* M. K. Young, technical editor. Conservation assessment for inland cutthroat trout. USDA, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

McRae, G. and C. J. Edwards. 1994. Thermal characteristics of Wisconsin headwater streams occupied by beaver: implications for brook trout habitat. Transactions of the American Fisheries Society 123:641-656.

Meisner, J. D. 1990a. Effect of climatic warming on the southern margins of the native range of brook trout, *Salvelinus fontinalis*. Canadian Journal of Fisheries and Aquatic Sciences 47:1065-1070.

Meisner, J. D. 1990b. Potential loss of thermal habitat for brook trout, due to climatic warming, in two southern Ontario streams. Transactions of the American Fisheries Society 119:282-291.

Meyer, K. A., D. J. Schill, F. S. Elle, and J. A. Lamansky. 2003. Reproductive demographics and factors that influence length at sexual maturity of Yellowstone cutthroat trout in Idaho. Transactions of the American Fisheries Society 132:183-195.

Meyer, K. A., D. J. Schill, J. A. Lamansky, M. R. Campbell, and C. C. Kozfkay. 2006. Status of Yellowstone cutthroat trout in Idaho. Transactions of the American Fisheries Society 135:1329-1347.

Miller, R. B. 1953. Comparative survival of wild and hatchery-reared cutthroat trout in a stream. Transactions of the American Fisheries Society 83:120-130.

Miller, R. R., J. D. Williams, and J. E. Williams. 1989. Extinctions of North American fishes during the past century. Fisheries 14:22-38.

Moyle, P. B. and T. Light. 1996. Biological invasions of fresh water: empirical rules and assembly theory. Biological Conservation 78:149-161.

Nelson, R. L., W. S. Platts, D. P. Larsen, and S. E. Jensen. 1992. Trout distribution and habitat in relation to geology and geomorphology in the North Fork Humboldt River drainage, northeastern Nevada. Transactions of the American Fisheries Society 121:405-426.

Nilsson, N. A. 1967. Interactive segretation between fish species. Pages 295-313 in S. D. Gerking, editor. The biological basis of freshwater fish production. John Wiley and Sons, New York, New York.

Nislow, K. H., C. L. Folt, D. L. Parrish. 2000. Spatially explicit bioenergetic analysis of habitat quality for age-0 Atlantic salmon. Transactions of the American Fisheries Society 129:1067-1081.

Novinger, D. C. 2000. Reversals in competitive ability: do cutthroat trout have a thermal refuge from competition with brook trout? Doctoral dissertation, University of Wyoming, Laramie, Wyoming.

Novinger, D. C. and F. J. Rahel. 2003. Isolation management with artificial barriers as a conservation strategy for cutthroat trout in headwater streams. Conservation Biology 17:772-781.

Ojanguren, A. F., F. G. Reyes-Gavilan, and F. Brana. 2001. Thermal sensitivity of growth, food intake and activity of juvenile brown trout. Journal of Thermal Biology 26:165-170.

Pauchard, A. and P. B. Alaback. 2004. Influence of elevation, land use, and landscape context on patterns of alien plant invasions along roadsides in protected areas of South-Central Chile. Conservation Biology 18:238-248.

Paul, A. J., and J. R. Post. 2001. Spatial distribution of native and nonnative salmonids in streams of the eastern slopes of the Canadian Rocky Mountains. Transactions of the American Fisheries Society 130:417-430.

Peterson, D. P. and K. D. Fausch. 2003. Testing population-level mechanisms of invasion by a mobile vertebrate: a simple conceptual framework for salmonids in streams. Biological Invasions 5:239-259.

Peterson, D. P., K. D. Fausch, and G. C. White. 2004. Population ecology of an invasion: effects of brook trout on native cutthroat trout. Ecological Applications 14:754-772.

Petty, J. T., P. J. Lamothe, and P. M. Mazik. 2005. Spatial and seasonal dynamics of brook trout populations inhabiting a central Appalachian watershed. Transactions of the American Fisheries Society 134:572-587.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D, and the R Core team. 2008. nlme: linear and nonlinear mixed effects models. R package version 3.1-89, R Foundation for Statistical Computing, Vienna, Austria.

Pino, J., X. Font, J. Carbo, M. Jove, and L. Pallares. 2005. Large-scale correlates of alien plant invasion in Catalonia (NE of Spain). Biological Conservation 122:339-350.

Platts, W. S. 1979. Relationships among stream order, fish populations, and aquatic geomorphology in an Idaho river drainage. Fisheries 4:5-9.

Pope, K. L. and C. G. Kruse. 2007. Condition. Pages 423-472 *in* C. S Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Power, G. 2002. Charrs, glaciations and seasonal ice. Environmental Biology of Fishes 64:17-35.

Pysek, P., V. Jarosik, and T. Kucera. 2002. Patterns of invasion in temperate nature reserves. Biological Conservation 104:13-24.

R Development Core Team. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Rahel, F. J. 2000. Homogenization of fish faunas across the United States. Science 288:854-856.

Rahel, F. J. 2002. Homogenization of freshwater faunas. Annual Review of Ecology and Systematics 33:291-315.

Reinthal, P. N. and M. L. J. Stiassny. 1991. The freshwater fishes of Madagascar: a study of an endangered fauna with recommendations for a conservation strategy. Conservation Biology 5:231-243.

Rieman, B. E. and K. Apperson. 1989. Status and analysis of salmonid fisheries: westslope cutthroat trout synopsis and analysis of fishery information. Project F-73-R-11, Subproject II, Job 1, Federal Aid in Fish Restoration, Idaho Department of Fish and Game, Boise.

Riley, S. C. and K. D. Fausch. 1992. Underestimation of trout population size by maximum-likelihood removal estimates in small streams. North American Journal of Fisheries Management 12:768-776.

Riley, S. C., K. D. Fausch, and C. Gowan. 1992. Movement of brook trout (*Salvelinus fontinalis*) in four small subalpine streams in northern Colorado. Ecology of Freshwater Fish 1:112-122.

Rodriguez, M. A. 2002. Restricted movement in stream fish: the paradigm is incomplete, not lost. Ecology 83:1-13.

Roghair, C. N. 2005. Brook trout movement during and after recolonization of a naturally defaunated stream reach. North American Journal of Fisheries Management 25:777-784.

Roni, P., A.H. Fayram, and M.A. Miller. 2005. Monitoring and evaluating instream habitat enhancement. Pages 209-236 *in* P. Roni, editor. Monitoring stream and watershed restoration. American Fisheries Society, Bethesda, Maryland.

Roni, P., editor. 2005. Monitoring stream and watershed restoration. American Fisheries Society, Bethesda, Maryland.

Rosenfeld, J. 2003. Assessing the habitat requirements of stream fishes: an overview and evaluation of different approaches. Transactions of the American Fisheries Society 132:953-968.

Rosenfeld, J., M. Porter, and E. Parkinson. 2000. Habitat factors affecting the abundance and distribution of juvenile cutthroat trout (*Oncorhynchus clarki*) and coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 57:766-774.

Rosenfeld, J. S. and S. Boss. 2001. Fitness consequences of habitat use for juvenile cutthroat trout: energetic costs and benefits in pools and riffles. Canadian Journal of Fisheries and Aquatic Sciences 58:585-593.

Ross, S. T. 1986. Resource partitioning in fish assemblages: a review of field studies. Copeia 1986:352-388.

Ross, S. T. 1991. Mechanisms structuring stream fish assemblages -are there lessons from introduced species. Environmental Biology of Fishes 30:359-368.

Roughgarden, J. 1979. Theory of population genetics and evolutionary ecology: an introduction. MacMillan , New York, New York.

Rupp, R. S. 1954. Beaver-trout relationship in the headwaters of Sunkhaze Stream, Maine. Transactions of the American Fisheries Society 84:75-85.

Sakai, a. K., F. W. Allendorf, J. S. Holt, D. M. Lodge, J. Molofsky, K. A. With, S. Baughman, R. J. Cabin, J. E. Cohen, N. C. Ellstrand, D. E. McCauley, P. O'Neil, I. M. Parker, J. N. Thompson, and S. G. Weller. 2001. The population biology of invasive species. Annual Review of Ecology and Systematics 32:305-332.

Schroeter, R. E. 1998. Segregation of stream dwelling Lahontan cutthroat trout and brook trout: patterns of occurrence and mechanisms for displacement. Master's thesis, University of Nevada, Reno, Nevada.

Shemai, B., R. Sallenave, and D. E. Cowley. 2007. Competition between hatchery-raised Rio Grande cutthroat trout and wild brown trout. North American Journal of Fisheries Management 27:315-325.

Shepard, B. B. and L. Nelson. *In prepartion*. Conservation of westslope cutthroat trout by removal of brook trout using electrofishing.

Shepard, B. B., B. E. May, and W. Urie. 2005. Status and conservation of westslope cutthroat trout within the western United States. North American Journal of Fisheries Management 25:1426-1440.

Shepard, B. B., K. L. Pratt, and P. J. Graham. 1984. Life histories of westslope cutthroat and bull trout in the upper Flathead River Basin, Montana. Final Report for EPA under contract Number R008224-01-5 prepared by Montana Department of Fish, Wildlife and Parks, Helena, Montana.

Shepard, B. B., B. Sanborn, L. Ulmer, and D. C. Lee. 1997. Status and risk of extinction for westslope cutthroat trout in the upper Missouri River Basin, Montana. North American Journal of Fisheries Management 17:1158-1172.

Shepard, B. B., M. Taper, R. G. White, and S. C. Ireland. 1998. Influence of abiotic and biotic factors on abundance of stream-resident westslope cutthroat trout Oncorhynchus clarki lewisi in Montana streams. Final report to USDA Forest Service, Rocky Mountain Research Station, Boise, Idaho for contract INT-92682-RJVA. Montana Cooperative Fishery Research Unit, Montana State University, Bozeman.

Shepard, B. B., R. Spoon, and L. Nelson. 2003. A native westslope cutthroat trout population responds positively after brook trout removal and habitat restoration. Intermountain Journal of Sciences 8(3):191-211.

Smith, M. W. and J. W. Saunders. 1958. Movements of brook trout, *Salvelinus fontinalis* (Mitchill), between and within fresh and salt water. Journal of the Fisheries Research Board of Canada 15:1403-1449.

Spens, J., A. Alanara, and L. O. Eriksson. 2007. Nonnative brook trout (*Salvelinus fontinalis*) and the demise of native brown trout (*Salmo trutta*) in northern boreal lakes: stealthy, long-term patterns? Canadian Journal of Fisheries and Aquatic Sciences 64:654-664.

Stapp, P. and G. D. Hayward. 2002. Effects of an introduced piscivore on native trout: insights from a demographic model. Biological Invasions 4:299-316.

Stewart, D. J. and F. P. Binkowski. 1986. Dynamics of consumption and food conversion by Lake Michigan alewives: an energetics-modeling synthesis. Transactions of the American Fisheries Society 115:643-661.

Stoneman, C. L. and M. L. Jones. 2000. The influence of habitat features on the biomass and distribution of three species of southern Ontario stream salmonines. Transactions of the American Fisheries Society 129:639-657.

Strahler, A. N. 1957. Quantitative analysis of watershed geomorphology. Transactions of the American Geophysical Union 38:913-920.

Strauss, R. E. 1979. Reliability estimates for Ivlev's electivity index, the forage ratio, and a proposed linear index of food selection. Transactions of the American Fisheries Society 108: 344-352.

Taniguchi, Y. and S. Nakano. 2000. Condition-specific competition: implications for the altitudinal distribution of stream fishes. Ecology 81:2027-2039.

Taniguchi, Y., K. D. Fausch, and S. Nakano. 2002. Size-structured interactions between native and introduced species: can intraguild predation facilitate invasion by stream salmonids? Biological Invasions 4:223-233.

Taylor, E. B. 2004. An analysis of homogenization and differentiation of Canadian freshwater fish faunas with an emphasis on British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 61:68-79.

Taylor, E. B., M. D. Stamford, and J. S. Baxter. 2003. Population subdivision in westslope cutthroat trout (*Oncorhynchus clarki lewisi*) at the northern periphery of its range: evolutionary inferences and conservation implications. Molecular Ecology 12:2609-2622.

Thomas, H. M. 1996. Competitive interactions between native and exotic trout species in a high mountain stream. Master's thesis, Utah State University, Logan, Utah.

Thompson, D. 2004. Competitive interactions between the invasive European honey bee and native bumble bees. Ecology 85:458-470.

Townsend, C. R. 1996. Invasion biology and ecological impacts of brown trout *Salmo trutta* in New Zealand. Biological Conservation 78:13-22.

Van Deventer, J. S. and W. S. Platts. 1989. Microcomputer software system for generating population statistics from electrofishing data - User's guide for Microfish 3.0. General Technical Report INT-254. USDA Forest Service, Intermountain Research Station, Ogden, Utah.

Van Winkle, W., K. A. Rose, B. J. Shuter, H. I. Jager, and B. D. Holcomb. 1997. Effects of climatic temperature change on growth, survival, and reproduction of rainbow trout: predictions from a simulation model. Canadian Journal of Fisheries and Aquatic Sciences 54:2526-2542.

Vander Zanden, M. J., J. D. Olden, J. H. Thorne, and N. E. Mandrak. 2004. Predicting occurrences and impacts of smallmouth bass introductions in North Temperate lakes. Ecological Applications 14:132-148.

Vander Zanden, M. J., J. M. Casselman, and J. B. Rasmussen. 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. Nature 401:464-467.

Varley, J. D. and R. E. Gresswell. 1988. Ecology, status, and management of the Yellowstone cutthroat trout. Pages 13-24 *in* Gresswell, R.E., editor. Status and management of interior stocks of cutthroat trout. American Fisheries Society, Bethesda, Maryland.

Vincent, R. E. and W. H. Miller. 1969. Altitudinal distribution of brown trout and other fishes in a headwater tributary of the South Platte River, Colorado. Ecology 50:464-466.

Weatherley, N. S., E. W. Campbellendrum, and S. J. Omerod. 1991. The growth of brown trout (*Salmo trutta)* in mild winters and summer droughts in upland Wales – model validation and preliminary predictions. Freshwater Biology 26:121-131.

Weatherly, A. H. and S. C. Rogers. 1978. Some aspects of age and growth. Pages 52-74 i*n* S. D. Gerking, editor. Ecology of freshwater fish production. Blackwell Scientific Publications, Oxford.

White, G. C., D. R. Anderson, K. P. Burnham and others. 1982. Capture-recapture and removal methods for sampling closed populations. UC-11, LA-8787-NERP. Prepared by U.S. Department of Energy, Los Alamos National Laboratory, Los Alamos, New Mexico.

Winkle, P. L., W. A. Hubert, and F. J. Rahel. 1990. Relations between brook trout standing stocks and habitat features in beaver ponds in southeastern Wyoming. North American Journal of Fisheries Management 10:72-79.

Wissinger, S. A., A. R. Mcintosh, and H. S. Greig. 2006. Impacts of introduced brown and rainbow trout on benthic invertebrate communities in shallow New Zealand lakes. Freshwater Biology 51:2009-2028.

Wofford, J. E. B., R. E. Gresswell, and M. A. Banks. 2005. Influence of barriers to movement on within-watershed genetic variation of coastal cutthroat trout. Ecological Applications 15:628-637.

Young, K. A. 2003. Evolution of fighting behavior under asymmetric competition: an experimental test with juvenile salmonids. Behavioral Ecology 14(1):127-134.

Young, K. A. 2004. Asymmetric competition, habitat selection, and niche overlap in juvenile salmonids. Ecology 85:134-149.